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Biometric variation among two Mangrove Warbler Setophaga petechia populations of Northwestern Mexico

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BIOMETRIC VARIATION AMONG TWO MANGROVE WARBLER *SETOPHAGA PETECHIA* POPULATIONS OF NORTHWESTERN MEXICO

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ABSTRACT

BIOMETRIC VARIATION AMONG TWO MANGROVE WARBLER *SETOPHAGA PETECHIA* POPULATIONS OF NORTHWESTERN MEXICO

CHERYL SCHWEIZER

Mangrove forests are one of the most productive ecosystems in the world. Despite this, over half of the world's mangroves have been lost, primarily due to anthropogenic activities. Northwestern Mexico is the northernmost range of mangroves in the eastern Pacific and western hemisphere. Mangrove Warblers (*Setophaga petechia castaneiceps* and *S. p. rhizophorae*), are small, tropical songbirds, endemic to these mangroves and are presumed to have sedentary lifestyles. Little is known about Mangrove Warblers across their range including basic life history data. Declining habitat across Mexico may be putting these populations at great risk. My primary objectives were to 1) define the biometric differences between and within the subspecies *S. p. castaneiceps* and *S. p. rhizophorae* and 2) determine local movement of a presumed sedentary mangrove bird.

In 2010-2011, I used playback and mist nets to capture, individually mark and measure 203 breeding adult Mangrove Warblers across their breeding ranges at 9 study areas in Baja California Sur and Sonora, Mexico. I summarized morphometric measurements using Principal Component Analysis (PCA) and performed Multivariate Analysis of Variance (MANOVA) to test if differences existed between subspecies, sex, and study areas. Results conclude *S. p. castaneiceps* is different from *S. p. rhizophorae (*P=<0.001), such that *S. p. castaneiceps* was a larger subspecies. Males were larger than females (P=<0.001) in both subspecies and variation existed among study areas in *S. p. castaneiceps* (P=0.001) and *S. p. rhizophorae* (P=<0.001). After finding significance among study areas, we then used SAS 9.2 to run MANOVA with post-hoc contrasts for each morphometric measurement within a subspecies. We found the Pacific Coast populations of *S. p. castaneiceps* to be generally larger than the western coast Sea of Cortez populations. The northernmost population for *S. p. rhizophorae* was smaller overall compared to the other populations sampled in Sonora.

The *S. p. castaneiceps* banded population was re-sighted during wintering (2010) and breeding (2011) periods to examine localized, year-round movements. Waypoints of breeding (2010 and 2011) and wintering (2010) locations were mapped and analyzed using ArcMap 9.3.1 to determine localized movements within the population. Results suggest the Mangrove Warbler has limited, if any, year-round movements. No movement was found among mangrove stands, but territory switching was found to occur within a mangrove stand between the wintering and breeding season. There was high territory replacement among the entire population suggesting that there may be high occurrence of floaters. Re-sighting surveys and capture events were used to calculate density of males, females and pairs per mangrove site. There were no significant changes in population density between seasons (P=0.07), but males averaged a higher year-round density compared to females and pairs (P=0.02).

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CHAPTER I

REVIEW OF LITERATURE RELEVANT TO STUDY

INTRODUCTION

Mangroves are one of the three most productive ecosystems in the world along with coral reefs and rain forests (Holguin et al. 2006). The Gulf of California is the northern edge for the distribution of mangroves in the Eastern Pacific and western hemisphere (Whitmore et al. 2005; Ruiz-Luna et al. 2010). Despite low human density in this area, there is increasing pressure on mangrove stands from anthropogenic activities (e.g. shrimp farming, rice cultivation, and urban development) which has led to localized destruction and fragmentation (Páez-Osuna et al. 2003; Brusca 2004; Glenn et al. 2006).

The mangrove forest of Baja California Sur and Sonora, Mexico is a mosaic of small islands as a result of habitat fragmentation due to increased pressures from human activities. In fact, within twenty years (1972-92) 65% of mangrove forests in Mexico were destroyed due to anthropogenic disturbance (Herrera-Silveira and Ceballos-Cambranis 2000), 70,000 ha lost between 1993 and 2000 (SEMARNAT 2003) (including 2,300 ha across Northwestern Mexico (early 1970's to 2005) (Ruiz-Luna et al. 2010)), and over 50% of mangroves have been destroyed worldwide (Holguin et al. 2006). Furthermore, this region is affected by seasonal hurricanes which cause considerable damage on mangrove forests by reducing overall stem density and basal area and uprooting trees (Kovac et al. 2001). Not only are tropical depressions common, but 78% of Mexico's total of hurricanes occur here (Flores-Verdugo et al. 1992). These influences combined with these weakened mangrove stands (e.g. exhibiting homogeneous tree structure and diversity, gaps or breaks in continuous vegetation, and poor health from lack of microbial benthic communities) in this area, present a great concern to study these unique habitats and preserve their biodiversity.

Few birds specialize in mangrove forests and detailed research of the ecology of the confined mangrove birds is sparse (Hogarth 1999; Luther and Greenberg 2009). The Mangrove Warbler (*Setophaga petechia castaneiceps* and *Setophaga petechia rhizophorae*, Fig 1.) is a small, tropical subspecies of the cosmopolitan Yellow Warbler (*Setophaga petechia*). It is a mangrove specialist and is endemic to the Pacific and Atlantic coasts of Mexico, Central and northern South America (Browning 1994). The nominate species, Yellow Warbler, is one of the most widespread of all warblers breeding from Alaska south to northwestern Peru (Curson et al. 1994). The generalization that temperate birds differ from tropical species in life-history traits, survivorship, and behavior is widely accepted. Despite these acceptances, foundational ecological data is absent for most tropical species.

The biometry of the Yellow Warbler has been well studied across its range (Wiedenfeld 1991), but only a few studies, consisting of limited samples on study skins, have been carried out on the Mangrove Warbler subspecies (S. p. spp.) in Mexico (Ridgeway 1885, 1902; Van Rossem 1935,1947). Often, variations in morphometric traits are coupled with variation in other morphological, physiological, and/or behavioral traits, both within and among species (Schluter and Smith 1986; Gustafsson 1988; Molina-Borja and Rodríguez-Domínguez 2004; Putnam and Flueck 2011). This variation in traits can influence survival and reproduction (Garland and Losos 1994; Rodriguero et al. 2002). Life-history of an individual can therefore be highly influenced by variation in morphometric traits. Biometric studies, in concurrence with other research, can be useful to further our understanding of the distribution and ecology of bird species and therefore improve conservation efforts (Atkinson et al. 1981; Telleria and Carbonell 1999; Campos et al. 2005).

This thesis is organized into three chapters that will present and discuss biometric variation in Mangrove Warbler populations in two areas of Northwestern Mexico. The first chapter is a review of background literature relevant to the entire study. The second chapter focuses on morphometric variation between and among two Mangrove Warbler subspecies, *S. p. castaneiceps* and *S. p. rhizophorae*. The third chapter examines year-round movement in the *S. p. castaneiceps* population with implications to territorial systems and breeding strategy. These chapters are designated as individual chapters, and written and formatted for the specifications of The Auk, the quarterly journal of the American Ornithology Union.

LITERATURE REVIEW

Taxonomics

The Yellow Warbler (*Setophaga petechia)*, a songbird within the wood warbler family Parulidae, order Passeriformes (Dunn and Garrett 1997), currently has 43 recognized subspecies (Browning 1994). Each of these subspecies fits into one of the three differentiated groups of the Yellow Warbler (American Ornithologist Union 1998): the *aestiva* group (Northern) which is migratory and breeds across North America, the *petechia* group (Golden) residing in the vicinity of the Caribbean Islands and West Indies, and the *erithachorides* group (Mangrove) found throughout mangroves on the Pacific and Atlantic coasts of Mexico, Central and northern South America (Browning 1994; Salgado-Ortiz et al. 2008; Fig. 2). Historically, each group was regarded as a distinct species with their names derived from the oldest described from each group; *Motacilla aestiva* (Gmelin 1789), *Motacilla petechia* (Linnaeus 1776) and *Dendroica erithachorides* (Baird 1858).

Browning (1994) recognized 16 subspecies of Mangrove Warblers in the *erithachorides* group (Fig. 1). Adult male Mangrove Warblers (*erithachorides* group) differ from the northern *aestevia* group chiefly by their rufous/chestnut hood (Curson et al. 1994; Howell and Webb 1995; Dunn and Garrett 1997; Pyle 1997). Unlike the *aestiva* and *petechia* groups who use variable types of habitats (Lowther et al. 1999), birds of the *erithachorides* group are restricted to coastal mangroves, especially Red Mangrove (*Rhizophora mangle*) (Hogarth 1999) throughout their range (Curson et al. 1994).

The separation of the groups has always boggled taxonomists. In the early 1900's, the entire complex was known as "Golden Warblers" with no apparent groupings (Ridgeway 1902). The species was also lumped together in multiple ways such as combining the *petechia* and *erithachorides* group as one species (Golden Warbler) and *aestiva* group as another species (Yellow Warbler) (Hellmayr 1935), and combining Hellmayr's Golden Warbler with the Yellow Warbler (Aldrich 1942) which reflects upon the current taxonomy. In addition, Klein and Brown (1994) suggested the division of the species into two groups based on their phylogenic study of Yellow Warblers using mitochondrial DNA. Their findings are consistent with those of Hellmayer (1935); one group consisting of migratory forms from North America (*aestiva* group) and the other consisting of the sedentary Mangrove and 'Golden' Warblers from the tropics (*erithachorides* and *petechia* groups).

Mangrove Warblers have long belonged to the genus *Dendroica*. Recent changes (15 April 2011) to classification and nomenclature have resulted in the sinking of the genus *Dendroica* and lumping with other genera to the genus *Setophaga* (American Ornithologists' Union 2011).

Morphometrics

Biometrics refers to any behavioral or physical characteristic that can be measured and statistically analyzed as a means for identifying or verifying an individual. Behavioral biometrics usually measure characteristics that are acquired naturally over a period of time. Some examples of behavioral biometrics include voice behavior such as songs in birds or whale calls and signature recognition in humans. Physical biometrics measures any physical characteristics of an individual. Usually these characteristics are related to the appearance of the body such as wing lengths of birds, fingerprints of humans, and color/pattern of hair. Analyzing DNA to obtain information about genetic makeup is a physical biometric.

The life-history traits of the northern migratory populations of Yellow Warblers have been extensively studied (e.g. Morse 1966; Lowther et al. 1999; Milot et al. 2000). The most recent literature describing physical biometrics of all Yellow Warbler subspecies is Browning (1994). The main purpose of his study was to evaluate geographic variation and to determine the morphological limits of the subspecies. The basis for his subspecies identification was from color and pattern of breeding plumages of adult males and females. Measurements were secondary in characterizing only a few subspecies. These specimens were study skins, some of which dated back to the 1800's.

Browning (1994) examined 63 Mangrove Warbler study skins from Baja California collected by Ridgeway (1885) and Van Rossem (1947). He described *D. p. castaneiceps* subspecific characters as nearest *rhizophorae* but slightly greener above, and males with chestnut streaks less dense and narrower. He also noted that male *castaneiceps* have slightly longer tails than *rhizophorae*. Browning (1994) further evaluated *D. p. rhizophorae* based on eight specimens from the state of Sonora, Mexico collected by Van Rossem (1935). He concluded

that this subspecies is slightly more yellow below than *castaneiceps*, and males have wider chestnut streaks and shorter tails.

Measurements for the *erithachorides* group were reported by Curson et al. (1994) from 16 male and seven female study skins. These measurements were taken from Ridgeway (1902), except for the wing lengths which were from Pyle et al. (1987). Male wing length was 53-70 mm, tail length 45-52 mm, bill length 11 mm, and tarsus 18-22 mm. Female wing length was 56-63 mm, tail length 45-47 mm, bill length 11 mm, and tarsus 17-22 mm. These results reflected individuals from differing subspecies throughout Central and South America, Caribbean, and the Galápagos Islands.

Mangrove Warblers are very similar to Yellow Warblers but average slightly larger and have a more rounded wing shape (primary 9 is shorter than primary 6). Generally, Mangrove Warblers are greener above and do not have as much yellow edging on wings. Female and immature Mangrove Warblers commonly show chestnut patches on various parts of the crown, face and throat, but are closely related to the plumages of female and immature Yellow Warblers (Lowther et al. 1999).

Breeding Ecology

Sedentary tropical birds often lay small clutches and have long incubation, nestling, and fledgling dependency periods for both sexes (Klopfer et al. 1974). They also typically have longer breeding seasons (Ricklefs 1969a). It is common of tropical resident birds to actively defend feeding territories (Cox 1985; Greenberg and Gradwohl 1986), and unlike most migratory species, for females to engage in territorial singing (Thorpe 1972; Catchpole and Slater 1995). Tropical birds generally have low nesting success (Skutch 1966; Ricklefs 1969b) and high adult

survivorship (Fogden, 1972; Greenberg and Gradwohl 1986, 1997; Francis et al. 1999). Annual survivorship rates for temperate zone passerines, for example, are about 40-60%, whereas tropical birds are approximately 80%-90% (Ricklefs 1973).

Three studies examined the breeding ecology of Mangrove Warblers. Snow (1996) studied Mangrove Warbler subspecies in the Galápagos Islands (*D. p. aureola*), and Barrantes (1998) studied *D. p. xanthotera* in Costa Rica. For my study, I follow the timing of breeding events reported by Salgado-Ortiz et al. (2008, 2009) due to the location (latitude) of their study species being nearest to mine. They studied the breeding ecology of one Mangrove Warbler subspecies of the southeast coast (Yucatán Peninsula) Mexico, *D. p. bryanti*. Based on their findings, the breeding season spans three and a half months from mid-April to late-July. Territories average 0.77 ha in size and males defend territories year round. Density averages 10.6 pairs/10 ha and does not change between the breeding and non-breeding seasons. Nest building begins the second half of April and takes approximately five days. The average date of egg laying is May 18, with a full clutch consisting of 3 eggs. The number of nesting attempts is 1-5, averaging 1.8 per female. Nests were initiated as late as the end of July. The incubation period is 12-14 days with average date of hatching on 30 May. The nestling period is 11 days on average. The average date of fledging (for the first nest attempt) is 12 June. Fecundity declines and adult survival increases in Yellow Warblers from temperate to tropical environments (Salgado-Ortiz et al. 2008).

Mangroves of Northwestern Mexico

Mangroves (or mangals) are almost exclusively tropical (approximately between 30°N and 38°S) and limited by low temperatures (Hogarth 1999; Stuart et al. 2007; Ruiz-Luna et al.

2010). Mangroves are distributed below 26°N in the Gulf of Mexico up to 29°20´N in the Sea of Cortez, which is the northern edge of mangrove distribution in the Eastern Pacific and western hemisphere (Whitmore et al. 2005; Ruiz-Luna 2010). Mangroves in Northwestern Mexico border the coastline of the states of Nayarit, Sinaloa, Sonora, and Baja California Sur.

Three mangrove species occur in Northwestern Mexico, each belonging to a separate family; Black Mangrove (*Avicennia germinans*), White Mangrove (*Laguncularia racemosa*), and Red Mangrove (*Rhizophora mangle*) (Roberts 1989; Ruiz-Luna et al. 2010). Red mangrove is the most common mangrove found in Baja California (Roberts 1989). Mangroves in Northwestern Mexico rarely exceed 5 m in height (Felger et al. 2001). No consistent species distribution or assemblage is found throughout this area (Ruiz-Luna et al. 2010), however mangrove species generally occur along a seaward zonation of black mangrove in the shallowest water, white mangrove in the center of the stand, and red mangrove in the deepest water (Tomlinson 1986; Hogarth 1999; Felger et al. 2001).

Mangroves generally grow in an environment whose salinity is between that of fresh water and sea water (Hogarth 1999), but can grow and tolerate hypersaline water (Felger et al. 2001). They are adapted to being submerged in salt water and lack understory growth due to twice daily tidal cycles and periodic flooding events caused by seasonal storms. Resultantly, mangrove trees have developed various forms of aerial roots to obtain oxygen for respiration. Aerial roots of red mangrove diverge from the tree as much as 2 m above the ground (Hogarth 1999) which make it more flexible to live in water logged areas. Black and white mangroves exhibit a different root structure, such that they radiate shallow, horizontal roots underground equipped with vertical standing pneumatophores. The pneumatophores protrude from the mud

(some as high as 3m) and are the main mechanism for gas exchange with underground tissue (Hogarth 1999).

Mangrove forests, and resultantly their inhabitants, may be subject to more disturbance than other forests due to their exposure to typhoons, coastal erosion, and fluctuating river discharges, for example (Hogarth 1999). Increase in destruction from anthropogenic pressures (such as shrimp farming, rice cultivation and urban development) has further heighted concern for mangroves in Mexico (Páez-Osuna et al. 2003; Brusca 2004; Glenn et al. 2006). Throughout the last few years, there have been numerous mangrove protection laws enacted and amended in Mexico. In 2003, mangrove management in Mexico was regulated by the Mexican Official Norm (NOM-022-SEMARNAT-2003) which "established the specifications for preservation, conservation, sustainable use and restoration of the coastal wetlands in mangrove areas" (SEMARAT 2003). This law allowed for the enforcement of mangrove protection, until the agreement to add Article 4.43 in 2004 which states "the prohibition of work and activities set out in paragraphs 4.4 and 4.22 and the limits set out in paragraphs 4.14 and 4.16 may be excluded if there is a preventative report of environmental impact statement, or if the case establishes compensation arrangements for the benefit of wetlands and it obtains corresponding land use change authorization" (Diario Oficial de la Federación, 3 Mayo de 2004). This addition gained immediate attention from many environmental organizations spurring for additional actions and reviews of the article. In 2007 another article was added (Article 60 TER of the Wildlife General Law), in which "it is forbidden to remove, fill, transplant, prune, or conduct any work or activity which directly or indirectly affects mangroves" (Diario Oficial de la Federación, 1 Febrero de 2007). Under this addition, Mexico prohibited nearly all urban development that was harmful to mangrove ecosystems.

Habitat Islands

Islands can either be naturally occurring, such as oceanic or ponds, or can be created through landscape characteristics. Geographic barriers (vicariance) are a common cause of restricting interactions among/within populations (Fitzpatrick et al. 2009). Landscape features such as mountains, canyons, and water sources quickly set a boundary for a habitat patch and hinder migration. Habitat specialists, such as the Giant Conebill *(Oreomanes fraseri*) and Tawny Tit Spinetail *(Leptasthenura yanacensis)* of high-Andean *Polylepis* spp. forests, can be considered to live in islands due to their confinement to appropriate habitat (Cahill and Matthysen 2007).

Anthropogenic disturbance of continuously distributed populations also can lead to small and fragmented populations similar to the conditions of islands (Seppa and Laurila 1999; Andersen et al. 2004; Qie et al. 2011). Habitat fragmentation occurs when human land use alters natural landscapes leading to a reduction of total area (habitat loss), changes in patch configuration, and isolation of habitat remnants (Mitrovich et al. 2009; Richter 2009). Habitat fragmentation threatens the viability of populations (Saunders et al. 1991; Fahrig and Merriam 1994; Tilman et at. 1994; Burkey 1995; Groombridge and Jenkins 2002; Hanski 2011). Roads, houses, dams, and agricultural fields are all common examples of habitat fragmentation. As large areas of habitat are fragmented, the total habitat area is reduced and results in disjointed fragments of varying size (Smith 1990).

As populations become increasingly isolated on remnant habitat islands in areas of unsuitable habitat matrices (such as urban, suburban, and agricultural developments), they may not have any outside source populations for exchange of crucial information (e. g. genetic material and song types) (Cole 1981; Burkey 1995). Nature reserves can be considered habitat

islands, such that they are often salvaged regions in vastly disrupted areas. Habitat fragmentation, advanced through anthropogenic interactions, is one of the greatest threats to biodiversity and conservation. Populations in fragmented habitat also have to cope with edge effect where ratio of edge relative to the interior habitat is heightened (Lidicker and Koenig 1996; Primack 2010).

The edge effect is an ecological process affecting habitat patches that resulted from fragmentation, and it is a result of interactions between two neighboring ecosystems that are disconnected by an abrupt transition (Murcia 1995). Three types of edge effects have a variety of influences on a habitat island relative to the species inhabiting the area: direct abiotic, direct biotic, and indirect biotic (Saunders et al. 1991)

Abiotic edge effects include microclimatic changes in the environment such as sunlight, temperature, humidity, wind, and fire (Prugh et al. 2008; Primack 2010). Road networks, for example, offer huge obstacles for birds, not only due to habitat loss and fragmentation required to build the roads, but also due to abiotic edge effects they introduce to an ecosystem (Kociolek et al. 2011). Introduction of pollutants, artificial and natural light, and noise are all results of roads. Artificial lighting can affect avian singing, breeding (Kempenaers et al. 2010), molting and migration (de Molenaar et al. 2006). Noise can reduce various bird population densities (Peris and Pescador 2004) and richness, change age structure (Francis et al. 2009), and alter acoustic communication (Wood and Yezerinac 2006; Goodwin and Shriver 2010; Luther and Baptista 2010). In forest habitats, abiotic factors can affect the interior of the habitat up to 50m from the edge (Paton 1994).

Direct biotic edge effects are often determined by the tolerance of the focal species. These effects involve any changes to species abundance and distribution due to the changes in overall conditions near the edge of the habitat patch.

Indirect biotic edge effects involve conditions changing species interactions, such as predation, parasitism, and competition. Stray dogs (Chokri and Selmi 2011), cats (Balogh et al 2011), and rats (Delgado et al. 2001), for example, all have been found to negatively impact nest success of numerous bird species. Predators, nest parasites, and exotic plants can encroach 500m or more, into the interior of a habitat patch (Wilcove 1985, Falk et al. 2011).

Two significant factors influencing edge effect are the movement behavior of matrix predators in the edge and their abundance in the matrix habitat (Vergara and Hahn 2009). For instance, the dynamics of bird populations are strongly affected by edge effect which enables matrix nest predators (Robinson et al. 1995; Hartley and Hunter 1998; Vergara and Hahn 2009). The Brown Headed Cowbird (*Molothrus ater*) is a species of great concern due to its increased brood parasitism facilitated by using habitat edges as an invasion point into habitat interiors. Additionally, predators can trigger an Allee effect (Gascoigne and Lipcius 2004) because predation rates tend to increase at low nest densities (Vergara and Hahn 2009).

Movement

The territoriality system of Mangrove Warblers is presumed to be much like other tropical resident species of birds, maintaining year-round territoriality with permanent pair bonds (Greenberg and Gradwohl 1986; Lefebvre et al. 1992; Morton and Stutchbury 2000). Territories often are co-defended and remain with constant boundaries regardless of high turn-over of individuals (Cox 1985; Greenberg and Gradwohl 1986, 1997; Gorrell et al. 2005). Mangrove

Warblers usually tolerate migratory Yellow Warblers in their territories and direct most of their defense towards other Mangrove Warblers (Wiedenfeld 1992). In habitats with stable population density and year-long territorial birds, it is common that vacant territories are filled within a matter of hours (Greenberg and Gradwohl 1997; Morton et al. 2000; Fedy and Stutchbury 2004).

Territorial adults abandoning their territory and shifting to control neighboring established territories, hereafter territory switching, occurs in tropical resident birds, some more often depending on species. Greenberg and Gradwohl (1997) found territory switching to occur in 37% of their marked population of Checker-throated Antwrens, whereas Freed (1987) found movements were rare in adult tropical House Wrens with an established territory. Morton et al. (2000) proposed that territory switching may be driven by resource availability in neighboring territories.

A subspecies of Mangrove Warbler occurring in the Yucatán peninsula, Mexico, (*Dendroica petechia bryanti*), defends territories year round, forms permanent pair bonds, and maintains a stable population density year-round (Curson et al. 1994; Salgado-Ortiz et al. 2008). Density of this subspecies averaged 10.6 pairs/10 ha with territories having a mean size of 0.77ha and did not change between breeding and non-breeding season (Salgado-Ortiz et al. 2008). To my knowledge, no data confirming territory switching has been reported for Mangrove Warblers throughout their range.

Numerous methods are used to study movements and territorial systems in wildlife. Perhaps the most common method for studying movement in birds is through the use of color bands for individual identification. Many researchers have used color-marking and subsequent re-sighting to determine movement, territoriality and survivorship in populations. Greenberg and Gradwohl (1986), for example, re-sighted four species of color-marked antbirds (*Myrmotherula*

fulviventris, *Myrmotherula axillaris*, *Microrhopias quixensis*, and *Thamnophilus punctatus*), and put the locations on a grid system to quantify movement within a territory and among years. Morton and Stuchbury (2000) color-marked Dusky Antbirds (*Cercomacra tyrannina)* and used playback in various locations to determine territory boundaries. Hestbeck et al. (1991) studied movements to previous and new wintering locations in Canada Geese *(Branta canadensis)* from large scale capture-resighting data. In my study, I will be using color-marking of individuals to focus on localized movement within the *S. p. castaneiceps* populations.

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Fig. 1. Mangrove warbler subspecies. *Setophaga petechia castaneiceps* male (top left), *S. p. castaneiceps* female (top right), *S. p. rhizophorae* male (bottom left), *S. p. rhizophorae* (bottom right).

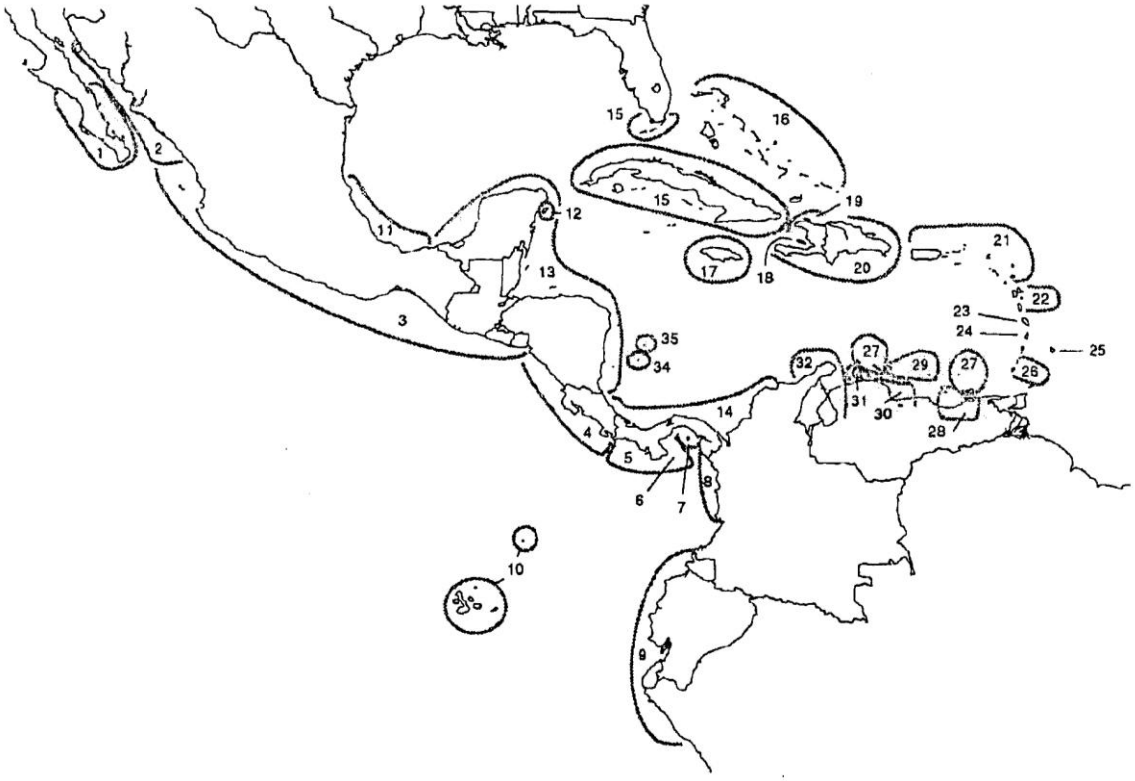

Fig. 2. Breeding ranges of *Setophaga petechia* in the *petechia* and *erithachorides* subspecies groups: 1, *castaneiceps*; 2, *rhizophorae*; 3, *phillipsi*; 4, *xanthotera*; 5, *aithocorys*; 6, *iguana*; 7, *aequatorialis*; 8, *jubaris*; 9, *peruviana*; 10, *aureola*; 11, *oraria*; 12, *rufivertex*; 13, *bryanti*; 14, *erithachorides*; 15, *gundlachi*; 16, *flaviceps*; 17, *eoa*; 18, *solaris*; 19, *chlora*; 20, *albicollis*; 21, *barthomelica*; 22, *melanoptera*; 23, *ruficapilla*; 24, *babad*; 25, *petechia*; 26, *alsiosa*; 27, *rufopileata*; 28, *aurifroms*; 29, *obscura*; 30, *cienagae*; 31, *paraguanae*; 32, *chrysendeta*; 33, *flavida*; 34, *armouri* (from Browning 1994).

CHAPTER II

MORPHOLOGICAL VARIATION BETWEEN MANGROVE WARBLER SUBSPECIES IN NORTHWESTERN MEXICO (*SETOPHAGA PETECHIA CASTANEICEPS* AND *S. P. RHIZOPHORAE*)

INTRODUCTION

Mangroves, coral reefs, and rain forests are the three most productive ecosystems in the world (Holguin et al. 2006). Mangroves are almost exclusively tropical (Hogarth 1999) and provide vital habitat for insects, coastal fish, birds, mammals, reptiles, and other marine species (Laegdsgaard and Johnson 1995; Hogarth 1999; Whitmore et al. 2005). Along with importance to flora and fauna, mangroves are fundamental to their ecosystems by absorbing contaminates from seawater (Tam and Wong 1995), improving seawater quality (Flores-Verdugo et al. 1992), and facilitating soil accretion (Young and Harvey 1996; Hogarth 1999). The soils of mangrove trees store organic carbon, making these ecosystems meaningful in mitigating climate change (Algoni et al. 2001). Mangroves also serve as a great importance to humans as far as alleviating impacts from tsunamis (Kathiresan and Rajendran 2005; Alongi 2008).

Mangroves are spread throughout the coastline of Mexico south of 26°N in the Gulf of Mexico and north to 29°20´ in the Gulf of California (Ruiz-Luna et al. 2010). The Gulf of California is the northern edge for the distribution of mangroves in the Eastern Pacific and western hemisphere (Whitmore et al. 2005; Ruiz-Luna et al. 2010). Despite low human density in this area, there is increasing pressure on mangrove stands from anthropogenic activities (e.g. shrimp farming, rice cultivation, and urban development) which has led to localized destruction and fragmentation (Páez-Osuna et al. 2003; Brusca 2004; Glenn et al. 2006). Within twenty years (1972-92), 65% of mangrove forests in Mexico were destroyed due to anthropogenic disturbance (Herrera-Silveira and Ceballos-Cambranis 2000), 70,000 ha lost between 1993 and 2000 (SEMARNAT 2003) (including 2,300 ha across Northwestern Mexico (early 1970's to 2005) (Ruiz-Luna et al. 2010)), and over 50% of mangroves have been destroyed worldwide (Holguin et al. 2006). Due to the historically isolated nature of mangroves and their importance

to ecosystem function, there is great need to study these unique habitats and preserve their biodiversity.

Throughout the last decade, numerous mangrove protection laws have been enacted and amended in Mexico. In 2003, mangrove management in Mexico was regulated by the Mexican Official Norm (standard: NOM-022-SEMARNAT-2003) which "established the specifications for preservation, conservation, sustainable use and restoration of the coastal wetlands in mangrove areas" (Diario Oficial de la Federación, 10 Abril de 2003). This law allowed for the enforcement of mangrove protection, until the agreement to add Article 4.43 (2004) which states "the prohibition of work and activities set out in paragraphs 4.4 and 4.22 and the limits set out in paragraphs 4.14 and 4.16 may be excluded if there is a preventative report of environmental impact statement, or if the case establishes compensation arrangements for the benefit of wetlands and it obtains corresponding land use change authorization" (Diario Oficial de la Federación, 3 Mayo de 2004). This addition gained immediate attention from many environmental organizations spurring for additional actions and reviews of the article. In 2007 another article was added (Article 60 TER of the Wildlife General Law), in which "it is forbidden to remove, fill, transplant, prune, or conduct any work or activity which directly or indirectly affects mangroves" (Diario Oficial de la Federación, 1 Febrero de 2007). Under this addition, Mexico prohibited nearly all urban development that was harmful to mangrove ecosystems. As with any legislation, however, there are many shortcomings, 'loopholes', and ways to manipulate these laws to satisfy personal interests resulting in mangrove harm and destruction. This has led to creating small, isolated patches of mangrove stands and consequently isolated populations of wildlife which inhabit this habitat.

Although some bird species opportunistically frequent mangroves, few birds specialize in these forests and detailed research of the ecology of confined mangrove birds is sparse (Hogarth 1999; Luther and Greenberg 2009). Mangrove Warblers (*Setophaga petechia castaneiceps* and *S. p. rhizophorae*) are small, tropical songbirds that are subspecies of the Yellow Warbler (*Setophaga petechia*). They are mangrove specialists and are endemic to the Pacific and Atlantic coasts of Mexico, Central and northern South America (Browning 1994). The nominate species, Yellow Warbler, is one of the most widespread of all warblers, breeding from Alaska south to northwestern Peru, including the Galapagos islands (Curson et al. 1994). The generalization that temperate birds differ from tropical species in life-history traits, survivorship, and behavior is widely accepted. Despite these acceptances, foundational ecological data are absent for most tropical species.

The biometry of the Yellow Warbler has been well studied across its range (Wiedenfeld 1991), but only a few studies, consisting of limited samples on study skins, have been carried out on the Mangrove Warbler subspecies (*S. p. spp*.) in Mexico (Ridgeway 1885, 1902; Van Rossem 1935,1947). Variations in morphometric traits are often coupled with variation in other morphological, physiological, and/or behavioral traits, both within and among species (Schluter and Smith 1986; Gustafsson 1988; Molina-Borja and Rodríguez-Domínguez 2004; Putnam and Flueck 2011). This variation in traits can influence survival and reproduction (Garland and Losos 1994; Rodriguero et al. 2002). Life-history of an individual can therefore be highly influenced by variation in morphometric traits. Biometric studies, in concurrence with other research, can be useful to further our understanding of the distribution and ecology of the Mangrove Warbler and therefore improve conservation efforts (Atkinson et al. 1981; Telleria and Carbonell 1999; Campos et al. 2005).

OBJECTIVE

The main objective of this study was to define the biometric differences between and within the subspecies *S. p. castaneiceps* and *S. p. rhizophorae*.

HYPOTHESIS

I hypothesize that the two subspecies, *S. p. rhizophorae* and *S. p. castaneiceps*, will vary in morphological traits. While I believe these two subspecies will be similar in many morphological measurements, I feel there will be certain characteristics that will be unique not only between subspecies, but also among the isolated populations inhabiting different study areas.

Ho: *S. p. castaneiceps* will not differ from *S. p. rhizophorae* in morphology

Ha: There will be a difference in morphology between *S. p. castaneiceps* and *S. p. rhizophorae*

I believe the adult male Mangrove Warblers of each subspecies will show significant differences from the adult females of their respective subspecies. I also believe there will be differences in mean morphological characteristics between the total adult populations of each study area when compared within a subspecies. I expect to find variation among the study areas for both *S. p. castaneiceps* and *S. p. rhizophorae*. Each of these hypotheses will be tested to examine the overall morphological differences between/within subspecies.

STUDY AREA

The study area included the known range of *S. p. castaneiceps* and *S. p. rhizophorae*. *S. p. castaneiceps* inhabits patches of mangroves from both coasts of central Baja California Sur from San Ignacio and Pond lagoons south to about 27°N on the Gulf of California (Browning 1994; Dunn and Garrett 1994). *S. p. rhizophorae* inhabits patches of mangrove on coastal Sonora from Tepopa Bay to Mazatlán, Sinaloa, Mexico (Browning 1994). Samples were only taken south to Yavaros, Sonora due to subspecies integration with *S. p. phillipsi* at Mazatlán (Browning 1994; Dunn and Garret 1997) and travel restrictions in Sinaloa, Mexico.

Baja California Sur and Sonora have an annual precipitation <300 mm and mean temperatures of 20-22°C (Ruiz-Luna et al. 2010) classifying this as an arid climate. Mangroves in this study are represented by three species, *Avicennia germinans* (black mangrove), *Rhizophora mangle* (red mangrove), and *Laguncularia racemosa* (white mangrove) (Hogarth 1999; Flores-Verdugo et al. 1992; Ruiz-Luna et al. 2010). Although there are no consistent patterns in species distribution or assemblage structure of mangroves in Mexico (Ruiz-Luna et al. 2010), study areas in Baja California Sur were dominated by red mangrove and black mangrove in Sonora. Mangrove trees in Baja California Sur and Sonora seldom exceed 5 m in height (Felger et al. 2001).

For *S. p. castaneiceps,* I placed study sites in Baja California Sur based on locations described in Whitmore et al. (2000). There were 18 study sites in Baja California Sur located within 5 major study areas: La Paz, Magdalena Bay, Puerto Adolfo López Mateos (hereafter referred to as PALM), Mulegé and San Lucas (Fig. 1-6). Fourteen sites were situated on the Sea of Cortez coastline. Each study site was designated as a mangrove stand separated by inhospitable habitat from the next closest stand.

All study sites on the west side of the Sea of Cortez were less than 1.8 km (straight line distance) across at greatest distance (length or width) and all were isolated patches separate from each other. All but one study site (LP6) on the Sea of Cortez coast for *S. p. castaneiceps* were <6 ha in total area (Table 1). Magdalena Bay is a large continuous mangrove stand on the Pacific Coast of Baja California Sur. It stretches (straight line distance) approximately 115 km along the coast. The entire study area for *S. p. castaneiceps* spanned a total straight line distance of 390 km and cumulative total area of 127.5 ha in Baja California Sur, Mexico. The overall average distance between neighboring study sites was 6.6km, but ranged from 0.9 km to 31.8 km (Table 1).

For *S. p. rhizophorae*, there were 13 study sites in Sonora, located within four major study areas: Bahia Kino, San Carlos, La Piedra, and Yavaros (Fig. 7-11). I assigned study sites to mangrove stands that were separated by inhospitable habitat from the next closest stand. All study sites run along the east coast of the Sea of Cortez and were less than 0.4 km (straight line distance) across at their widest point. All but three study sites were <6.2 ha in size (Table 1). The entire study area for *S. p. rhizophorae* spanned a total straight line distance of 339 km and cumulative total area of 74.1 ha in Sonora, Mexico. The overall average distance between neighboring study sites was 1.2 km, but ranged from <0.1 km to 9.4 km (Table 1).

METHODS AND MATERIALS

Data Collection

Mangrove Warblers were captured during the breeding season (March-July 2010 and 2011) at each study site in Baja California Sur and Sonora using mist nets and playback

recordings of their songs as a decoy. Within any study site, multiple locations (i.e. net lanes) were used to conduct necessary field work. I captured as many individuals as possible to maximize the sample size.

Each bird was banded with a U.S. Geological Service aluminum band and unique color combination (4 color plastic bands) for individual identification (Permit # 20580). The leg containing the federal band was marked with a color band corresponding to one of the major study areas. The other leg was marked with three color bands. At the time of capture, all locations were recorded via GPS unit with a minimum of 10 m accuracy. After processing, individuals were released at point of capture.

Age was determined through plumage and skull pneumatization (Howell and Webb 1995; Pyle 1997). Birds were categorized into hatch year (HY) and after hatch year (AHY) year classes. If identified, more detail was noted to further age individuals of AHY to either second year (SY) or after second year (ASY). Sex, male (M) or female (F), was determined through coloration and presence of brood patch/cloacal protuberance (Howell and Webb 1995; Pyle 1997). All individuals that were not capable of being sexed were classified as unknown (U). Skull pneumatization was based on a 0-6 scale, where 0 indicated no ossification and 6 indicated full ossification of the skull. A class 6 skull indicated an AHY individual.

Biometric Measurements

My measurements were made in accordance to Pyle (1997), unless noted. I took fat and breast muscle measurements to assess body condition. Sub-epidermal fat was measured by inspecting the abdomen and furcula of every bird. I assigned fat amounts to a class based on a 0-7 scale, where 0 was no fat present in the furcula and abdomen and a score of 7 was much fat

where nearly the entire ventral side of the bird is covered with fat, extending up to the neck and head (DeSante et al. 2008). Muscle was scored on a 0-3 scale where 0 corresponded to a prominent ridge on the sternum displaying depressed pectoral muscles (pectoralis major and pectoralis minor) and concavity of the pectoral muscles next to the keel. Well developed, enlarged pectoral muscles where the sternum was barely distinguished was scored as 3 (Bairlein 1995).

I measured unflattened wing chord measurements (0.5 mm) using a wing rule with a perpendicular stop at zero. Tail length was taken between the two central retrices (R6) from the base of the tail to tip of feather (0.5 mm). Total length of the bird measured from the tip of the bill to tip of the tail while the bird was straightened out on its back. The head was laid back flat against the ruler, neck not stretched, until the tip of the bill hit the perpendicular stop at zero (0.5 mm) (Svensson 1994).

Tarsus length was measured with vernier calipers when the foot was bent at a 90 degree angle towards the tarsometatarsal bone. Measurements were taken from the notch on the intertarsal joint to the distal end of the last leg scale before the toes begin. Bill length (exposed culmen) was measured from the tip of feathering at the base of the bill to the tip of the bill using vernier calipers (0.1 mm). Bill (culmen) depth was also measured with vernier calipers from the anterior edge of the nostrils to the notch in lower mandible (0.1 mm). Using a 30 g Pesola spring scale, I measured the weight of the birds to the nearest 0.1 g. I also took uniform photographs of each bird for reference and comparison.

Data Analyses

Only banded birds with data collected for each measurement variable were used for analysis. Birds that were of unknown age or sex were eliminated from analyses (1.6%). Prior to analyses, we tested variables for normality using a histogram. Variables were approximately normally distributed and all analyses were based on untransformed data. We summarized biometric measurements using Principal Component Analysis (PCA). We chose the first two principal components for regression analysis and graphical exploration based on eigenvalues (>1) and screeplot examination.

We performed Multivariate Analysis of Variance (MANOVA) to test if differences existed between subspecies, sex, and study areas. We used subspecies, sex, and study areas as the predictor variables and morphometric measurements as the response variables. These tests were completed using statistical software R (version 2.12.0).

For each subspecies, we then used statistical software SAS (version 9.2) to run MANOVA and ANOVA with post-hoc contrasts for each morphometric measurement (sex and age combined) with the study areas as the predictor variables. For the contrasts, the mean of a morphological measurement (e.g. mean wing chord) for a study area (e.g. La Paz) was compared to the mean of a morphological measurement of the combined remaining study areas (e.g. mean wing chord of all individuals in San Lucas, Mulegé, Magdalena Bay, and PALM). In *S. p. castanceips* we did a contrast combining the mean of Magdalena Bay and PALM against all other study areas because they were both situated on the Pacific Coast situated in fairly continuous mangrove stands compared to the highly fragmented and isolated mangrove stands on the Sea of Cortez. A result was significant when $p < 0.05$.

RESULTS

Capture Success

Overall in the *S. p. castaneiceps* subspecies, there were a total of 87 AHY males (72 ASY, 15 SY) and 42 AHY females (29 ASY, 13 SY) banded during the breeding season at a total of 74 capture locations within the 5 study areas. There were 63 AHY males (47 ASY, 5 SY) and 11 AHY females (10 ASY, 1 SY) *S. p. rhizophorae* individuals banded at a total of 48 capture locations within 4 study areas (Fig. 12).

Subspecies Comparison

S.p. castaneiceps and *S. p. rhizophorae* populations were clearly different based on morphometric measurements (F=63.91, dF=1, P=<0.001) (Table 2, Fig. 13). *S. p. castaneiceps* were larger than *S. p. rhizophorae*. Overall, the Mangrove Warblers (n=203) averaged a 63.7 mm wing chord, 11 mm bill length, 3.7 mm bill depth, 21.5 mm tarsus length, 50.6 mm tail length, 115.2 mm total length, 11.1g weight (Table 3).

The first two principal components explained 74% of the overall variance (PC1 57%, PC2 18%) between *S. p. castaneiceps* and *S. p. rhizophorae* (Table 4). PC1 describes the overall size of the bird, with highest factor loadings on total length, weight, wing chord and tarsus length, whereas PC2 describes primarily bill shape (Table 5).

Sex Comparison

Morphometric measurements were significantly different for sexes within each Mangrove Warbler subspecies (F=24.64, dF=1, P=<0.001) (Table 2). Males were larger than females overall, but were closely related in bill length, bill depth, and tarsus length (Table 3). There was no interaction between subspecies and sex (F=0.55, dF=1, P=0.79) (Table 2).

Age Class Comparison

Slight morphometric variation was found among age classes, such that ASY individuals (both males and females) were generally larger than SY individuals in *S. p. castaneiceps* and *S. p. rhizophorae*. Bill length, bill depth, and tarsus length had the least variation and most overlap between the age classes (Table 3).

Variation Among Study Areas

Morphometrics varied significantly among the *S. p. castaneiceps* study areas (F=1.95, dF=5, P=0.001) and among the *S. p. rhizophorae* study areas (F=2.97, dF=3, P=<0.001) (Table 6).

S. p. castaneiceps

Wing chord and bill depth did not differ among the study areas (Table 7). Bill length was significantly different among study area populations (F=4.14, dF=4, P<0.01) (Table 7, 8). La Paz and San Lucas populations had longer bill lengths, whereas PALM and the combined Magdalena Bay and PALM study areas averaged shorter bill lengths compared to the overall mean of the other study areas (Fig. 14). Tarsus length was significantly different overall (F= 2.76, dF=4, P=0.03) (Table 7), with specific difference existing between Magdalena Bay, San Lucas, and the combined Magdalena and PALM study areas (Table 9). Magdalena Bay and the combined Magdalena Bay and PALM study areas averaged a greater tarsus length whereas the San Lucas population exhibited a smaller mean tarsus length comparatively (Fig. 15). Tail length was not significant overall (Table 7), but was different for Magdalena Bay (F=7.48, dF=1, P<0.01) (Table 10) as it had a greater mean length (Fig. 16). Total length varied significantly among the study areas (F=2.85, dF=4, P=0.03) (Table 7) with differences existing between mean

total length of the Magdalena Bay (F=7.45, dF=1, P=<0.01) and the combined Magdalena Bay and PALM populations (F=7.04, dF=1, P=<0.01) (Table 11) such that they were larger (Fig. 17). Weight of the La Paz population was less (Fig. 18) and significantly different compared to the mean weight of the other study area populations (F=11.82, dF=1, P<0.001) (Table 12). The combined populations of Magdalena Bay and PALM were also significantly different (F= 8.70, dF= 1, P<0.01) (Table 12) as they had a greater weight comparatively (Fig. 18).

S. p. rhizophorae

Bill length and bill depth measurements did not differ among study areas (Table 13). Wing chord differed significantly overall among the study areas (F=6.13, dF=3, P=0.001) (Table 13) with San Carlos study area exhibiting a significantly larger mean wing chord and Bahia Kino study area a smaller mean wing chord (Table 14, Fig. 19). Tarsus length was not significant overall (Table 13), but was different for Yavaros (F=5.84, dF=1, P=0.02) (Table 15) as it had a greater mean length compared to the other study areas (Fig. 20). Tail length was significantly different among study areas (F= 7.58, dF=3, P=<0.001) (Table 13), but only varied for the Bahia Kino study area where tail length was shorter (Table 16, Fig. 21). Mean total length was significantly greater for San Carlos study area and shorter for Bahia Kino study area comparatively (Table 17, Fig.22). Weight was also significantly different among study area populations overall (Table 13). La Piedra had a slightly smaller mean weight and the Yavaros study area population had a greater mean weight (Table 18, Fig. 23).

DISCUSSION

Subspecies Comparison

Body size and its components are the targets of numerous selective processes (Price 1984; Brown and Brown 2011*).* Our research confirms *S. p. castaneiceps* and *S. p. rhizophorae* differ significantly in morphology. Individuals of *S. p. castaneiceps* are generally larger than individuals of *S. p. rhizophorae*, and both are greater in overall size than the northern Yellow Warbler (*S. p. aestiva*) (Widenfeld 1991; Pyle 1997). These differences are substantial and are distinguishable in the field, making it a helpful characteristic for distinguishing between the two subspecies (Cicero and Johnson 2006).

Our results agree with measurement results reported in Curson et al. (1994) for Mangrove Warblers, except for female tail length which was larger in our study. Our results also agree with subspecific characters in Browning (1994) stating *S. p. castaneiceps* tails are slightly larger than *S. p. rhizophorae*, however we found slightly smaller tails for *S. p. castaneiceps* comparatively. Tail length, however, was highly variable (as seen in boxplots) possibly due to differences in feather wear and molting conditions (Alonso and Arizaga 2006).

Increased body and bill size of passerine birds on islands has been well documented (i.e. Scott et al. 2003; Boyer and Jetz 2010; Greenberg and Olsen 2010) including in mangrove stands representing habitat islands (Luther and Greenberg 2011). Our research supports the idea of "island syndrome" (differences in demography, reproduction, behavior, and morphology compared to mainland populations) such that both Mangrove Warbler subspecies had longer and deeper bills and overall body size compared to Yellow Warblers (Curson et al. 1994; Pyle 1997; Lowther et al. 1999) Changes in bill size and shape are indicators of ecological pressures in local environments, particularly food resources and foraging behavior (Grant and Grant 2002;

Temeles et al. 2010). Increased bill size may be a result to generalization in resource use (Scott et al. 2003). These observations suggest the need to investigate the relationship between resource availability, habitat preference, and morphology within different mangrove stands in Northwestern Mexico.

Sex Comparison

The amount of sexual dimorphism in the avian taxa, along with the variety of features that have been subject to sexual selection, is extensive (Shutler and Weatherhead 1990; Andersson 1994). Many birds show sexual difference, usually in color (sexual dichromatism) or size (sexual dimorphism) (Siefferman et al. 2007; Igic et al. 2010), commonly exhibiting more colorful, brighter, and larger males.

Sexual dimorphism in *Setophaga* warblers varies from modest (such as the Yellow-throated Warbler (*Setophaga dominica*) exhibiting contrast primarily in dull colors and finer streaking) to extreme (such as in the Black-throated Blue Warbler (*Setophaga caerulescens*) in which the adult male is bright blue with black patches and the adult female is olive above and buffy below) (Dunn and Garrett 1994). Mangrove Warblers show sexual dimorphism in the presence of a rufous/chestnut head in males and through differences in size. Sex specific variation was observed for all measurements with males from both S. *p. castaneiceps* and *S. p. rhizophorae* being larger than females. Tarsus length, bill length, and bill depth measurements however, had very subtle differences between male and females. These differences may not be great due to selection that may act on body size. Males and females, especially in a sedentary, monogamous warbler, spend much of their lives living in close proximity to each other. Using

the same niche may require similar body characteristics in males and females (Gorrell et al. 2005).

Age Class Comparison

Our results agree with Lowther et al. (1999) research with Yellow Warblers, such that ASY birds (both males and females) have a greater weight than SY birds. Most distinct differences in age classes of passerines, in general, come from plumage and molt patterns rather than body measurements (Pyle 1997), especially between the ASY and SY age classes.

Age class is mostly important for breeding success such that older birds (ASY) are more successful than younger birds (SY) for reasons such as mate choice, song quality (Poesel et al. 2006),early arrival date, territory quality, and increased parental care at the nest (e.g. Cooper et al. 2009). A greater weight in ASY individuals may be a benefit in defending territories against SY individuals looking to establish a territory.

Variation Among Study Areas

Morphometric variation was observed among study areas of each Mangrove Warbler subspecies. Habitat characteristics have been shown to influence variation in morphometric measurements for numerous bird species (e.g. Arizaga et al. 2009; Desrochers 2010). In *S. p. castaneiceps*, the populations on the Pacific Coast (Magdalena Bay and PALM) showed the greatest contrast in morphometric measurements from the populations along the west coast of the Sea of Cortez (La Paz, Mulege, and San Lucas). Generally, the Pacific Coast populations had overall larger body features (tarsus length, tail length, total length, and weight) but smaller bill sizes compared to the Sea of Cortez populations. The Pacific Coast of Baja

California Sur has cooler temperatures and receives more rainfall annually compared to the Sea of Cortez coast (Brusca 2010) which may be a driving force for morphological variation (Wiedenfeld 1991). Differences in mean temperatures and precipitation can account for changes in environmental conditions such as vegetation, habitat structure, resource availability, and predator presence, which may drive changes in morphology of local populations (Telleria and Carbonell 1999).

S. p. rhizophorae showed a consistent pattern of smaller sized individuals in Bahia Kino (decreased wing length, tail length, and total length) compared to the other study areas in Sonora. The Bahia Kino population was the northern most study area we sampled. As the eastern coast of the Sea of Cortez follows a southward rising temperature gradient and rainfall amount, response of morphological measurements to changes in environment may be occurring (Peinado et al. 2010).

Speciation can occur quickly with high diversity of resources, even with little or no geographical separation (Price 2008). Variation may be explained by various selective pressures (e. g. resources, competition, predation, sexual selection) acting on individual habitat islands (study areas) which might result in changes in life history (Santiago-Alarcon and Parker 2007).

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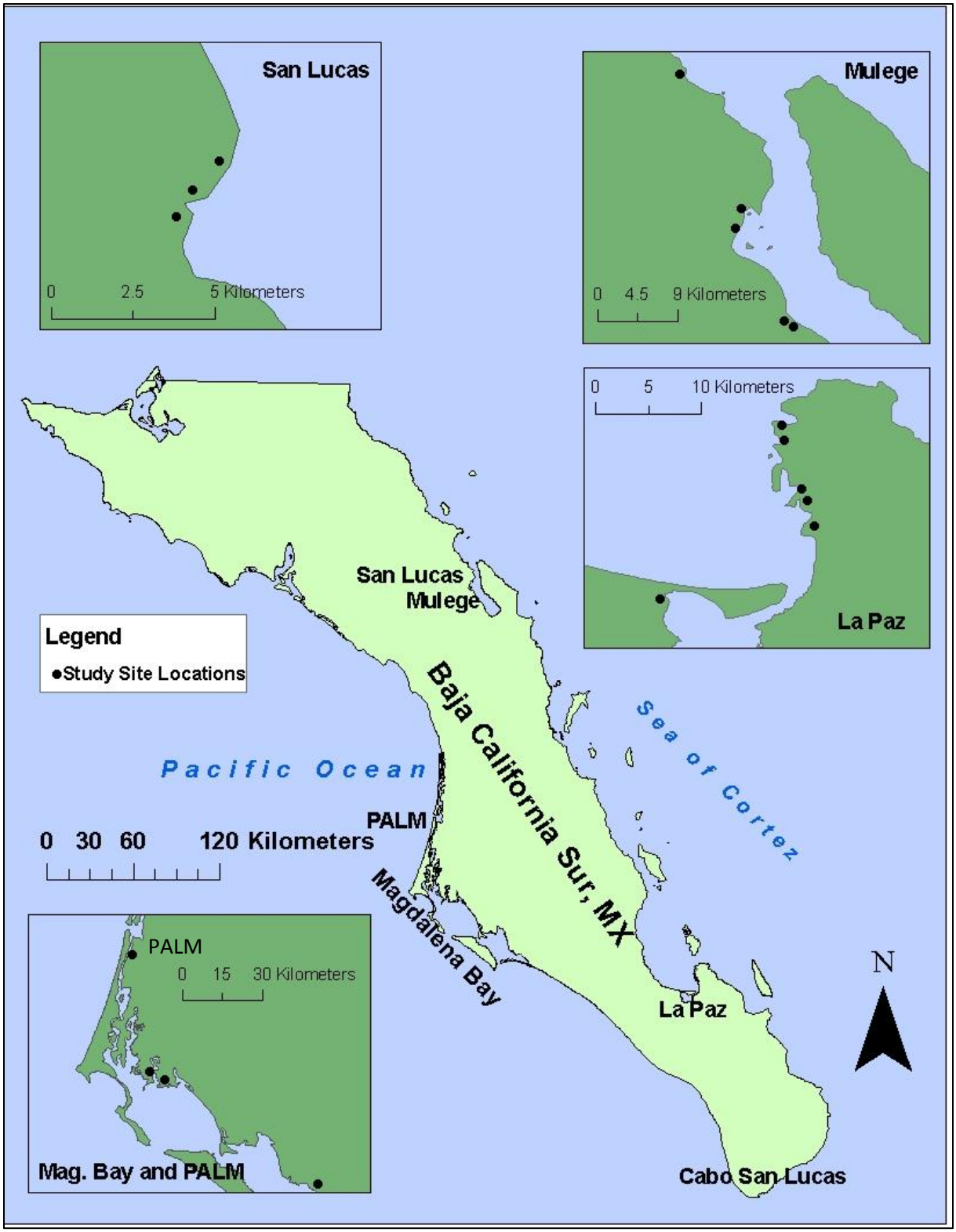

Fig. 1. Distribution and study site locations of *S. p. castaneiceps*, Baja California Sur, Mexico, with details showing five major study areas (San Lucas, Mulegé, Puerto Adolfo López Mateos (PALM), Magdalena Bay, and La Paz) and study sites within the major study areas.

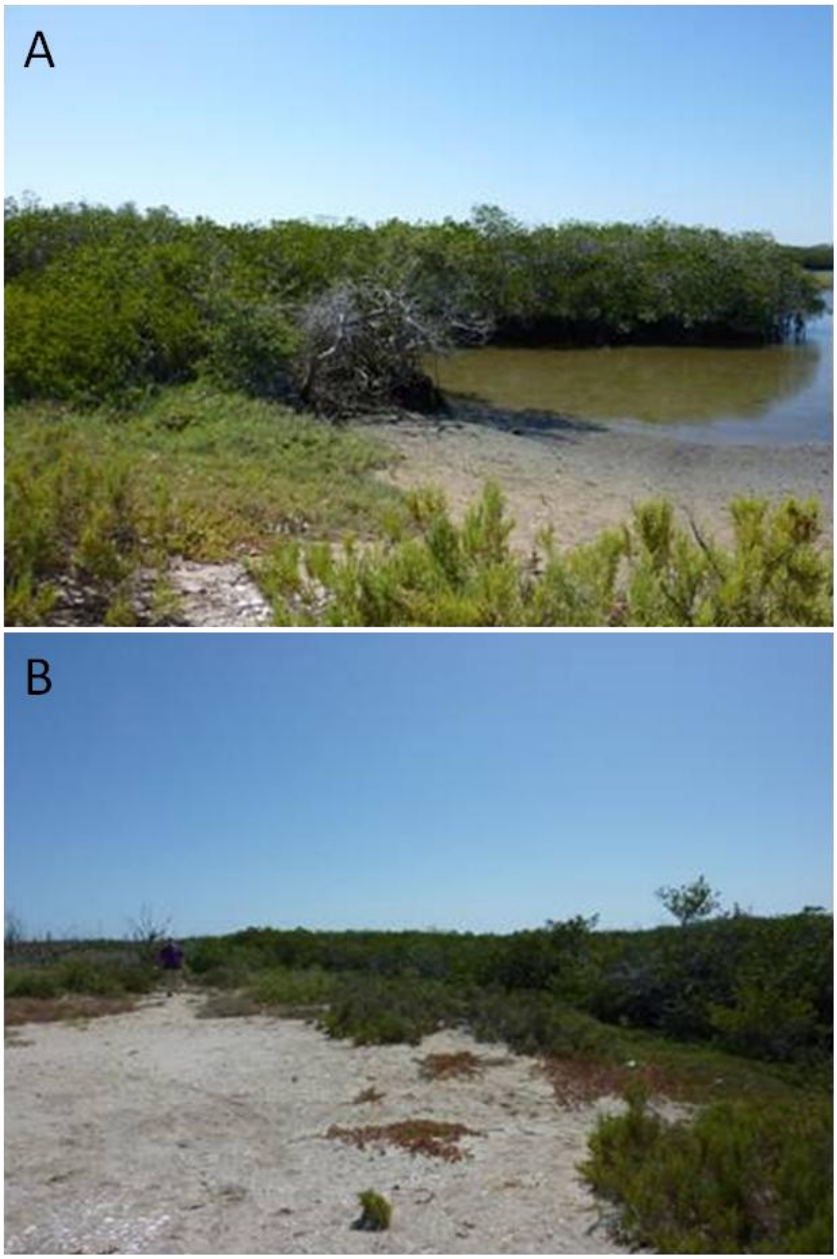

Fig. 2. Magdalena Bay study area, Baja California Sur, Mexico, from lagoon (A) and interior (B).

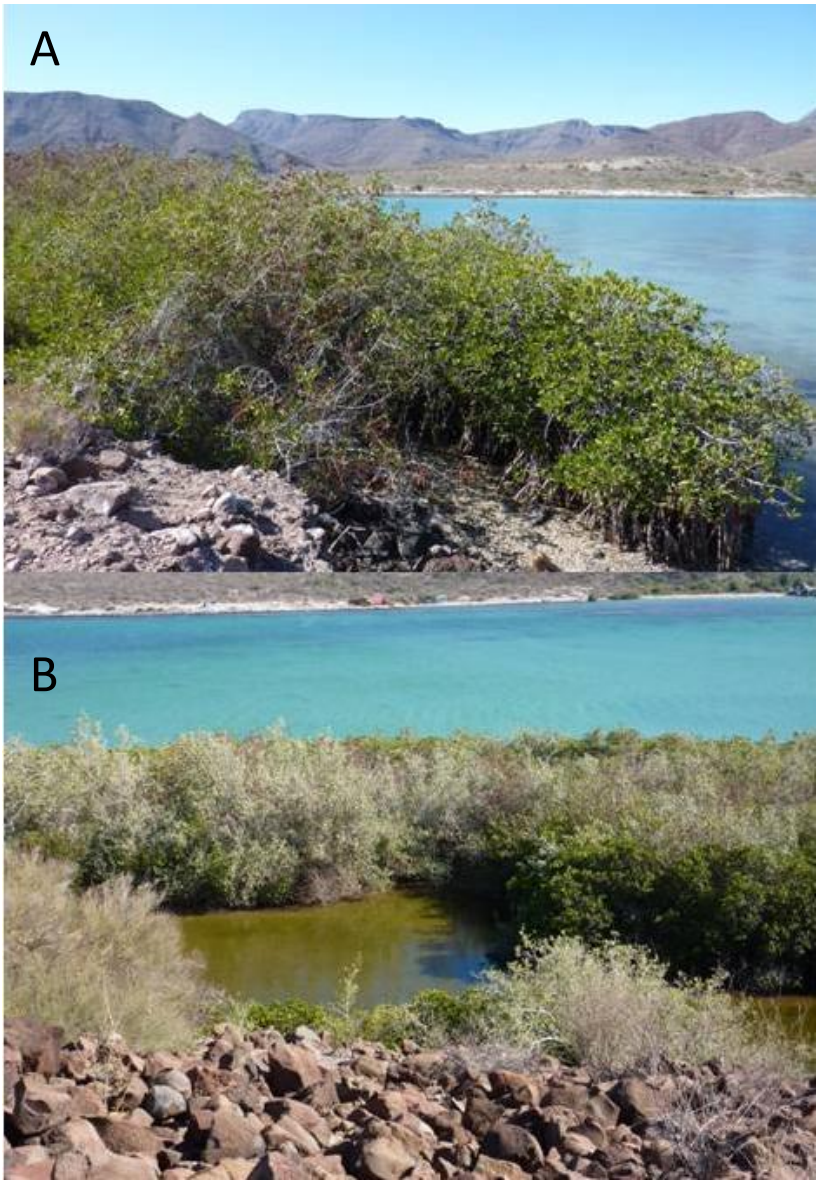

Fig. 3. Mulegé study area, Baja California Sur, Mexico from coast (A) and showing common brackish lagoons within mangrove stands (B).

Fig. 4. San Lucas study area, Baja California Sur, Mexico.

Fig. 5. Puerto Adolfo López Mateos (PALM) study area, Baja California Sur, Mexico from coast at low tide (A) and interior (B).

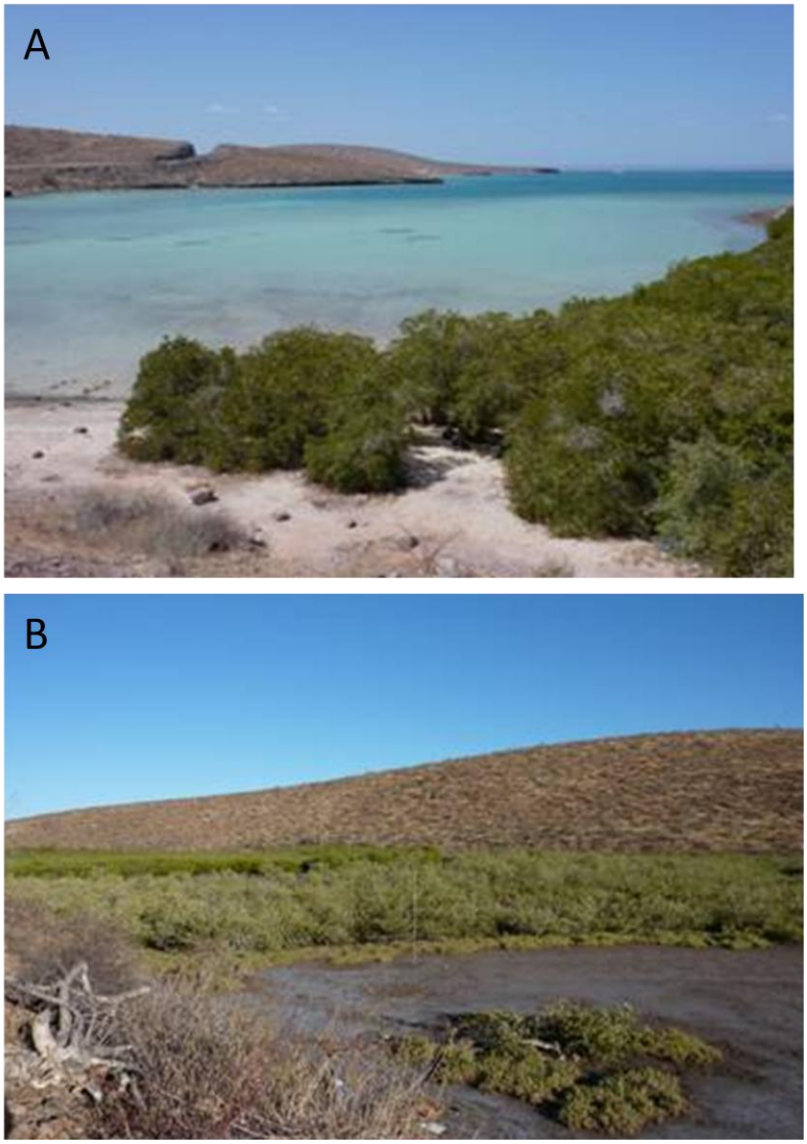

Fig. 6. La Paz study area. Baja California Sur, Mexico from coast (A) and interior (B).

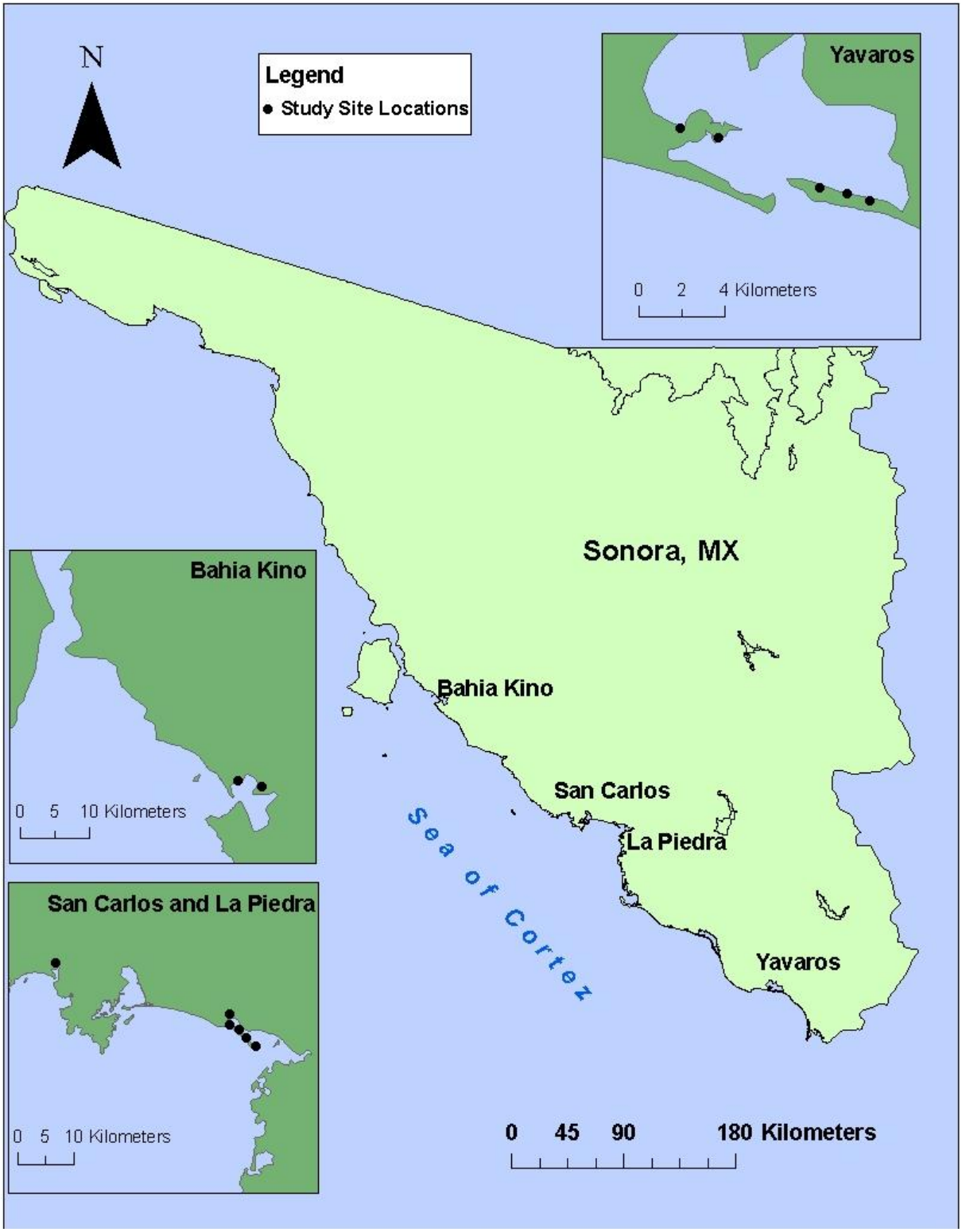

Fig 7. Distribution and study site locations of *S. p. rhizophorae*, Sonora, Mexico, with details showing four major study areas (Bahia Kino, San Carlos, La Piedra, and Yavaros) and study sites within the major study areas.

Fig. 8. San Carlos study area, Sonora, Mexico.

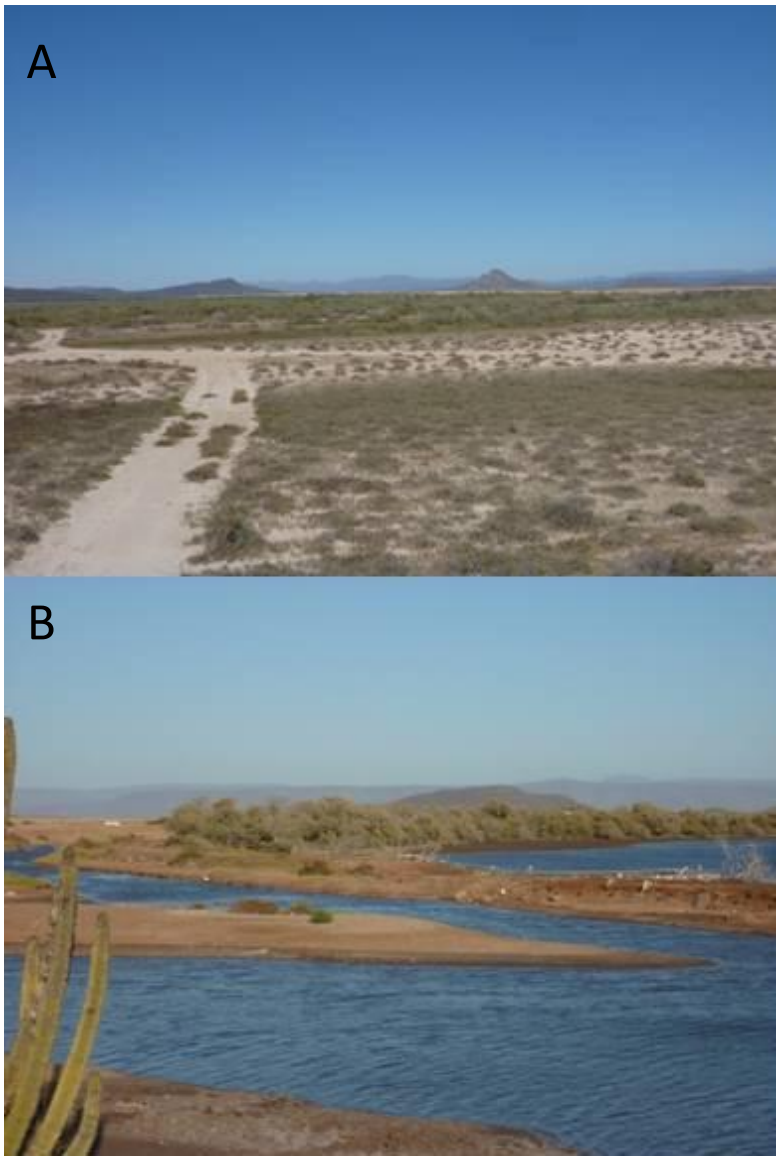

Fig. 9. La Piedra study area, Sonora, Mexico from interior (A) and coast (B).

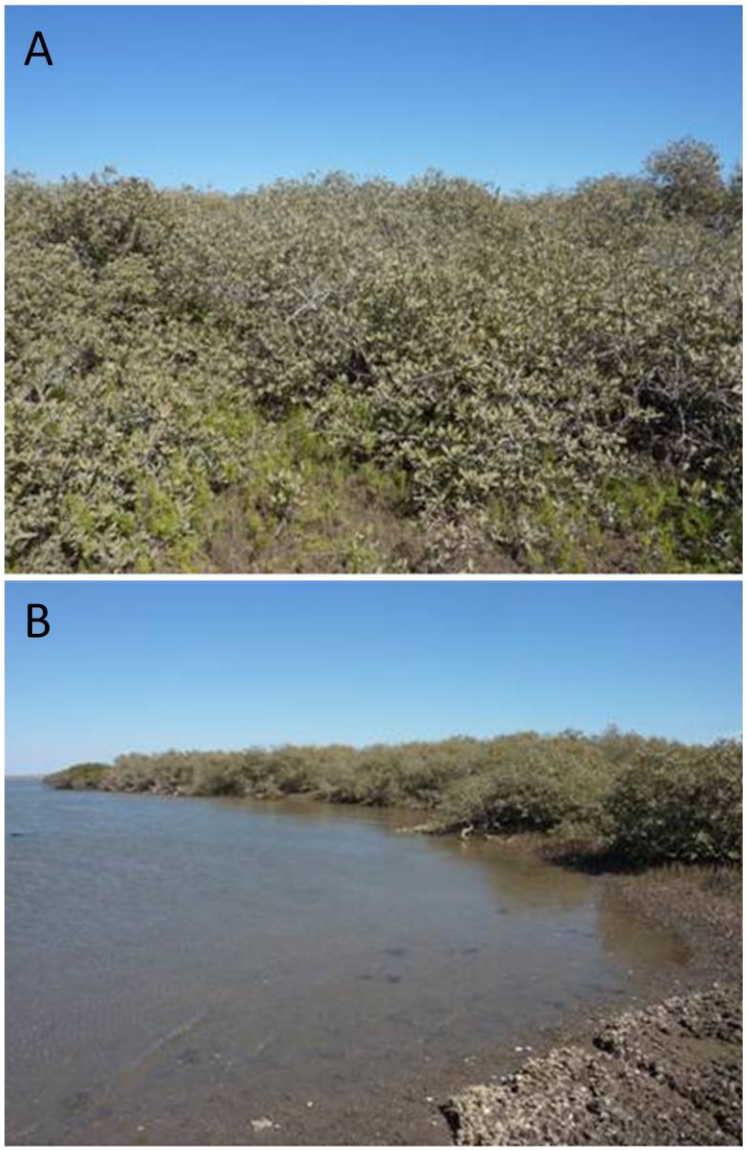

Fig. 10. Yavaros study area, Sonora, Mexico, from interior (A) and from coast (B).

Fig. 11. Bahia Kino study area, Sonora, Mexico.

Table 1. Area and perimeter of study areas and study sites in Baja California Sur and Sonora, Mexico. Straight-line distances (determined in ArcMap 9.3.1) between major study areas and minimum/maximum distances between study sites within a study area.

Major Study Area	Study Site Names	Total Area (ha)	Total Perimeter (km)	Max. Distance Between Study Sites (km)	Min. Distance Between Study Sites (km)	Average Distance Between Study Sites (km)
La Paz		40.48	21.04	19.42	0.91	5.72
	LP1	2.37	1.62			
	LP3	3.71	1.62			
	LP4	3.61	2.41			
	LP6	25.05	10.32			
	LP7	5.87	5.07			
Magdalena Bay		67.79	10.39	11.9	11.9	11.9
	MB1	25.87	7.1			
	MB3	41.91	3.29			
PALM		6.46	2.42	--	--	--
Mulege		8.77	8.53	31.81	1.83	8.01
	MU2	1.41	1.92			
	MU3	0.35	0.73			
	MU4	3.21	2.01			
	MU5	2.92	1.94			
	MU6	0.88	1.93			
San Lucas		4.04	3.3	1.94	0.95	0.95
	SL1	0.17	0.17			
	SL2	1.74	1.26			
	SL3	2.12	1.87			
Bahia Kino		22.77	9.86	1.12	1.12	1.12
	BK1	0.26	0.68			
	BK2	22.52	9.18			
San Carlos		15.08	10.38	--	--	--

Table 1. Continued

Major Study Area	Study Site Names	Total Area (ha)	Total Perimeter (km)	Max. Distance Between Study Sites (km)	Min. Distance Between Study Sites (km)	Average Distance Between Study Sites (km)
La Piedra		20.17	15.95	3.96	0.08	0.44
	PA1	0.57	0.5			
	PA2	1.49	6.25			
	PA3	3.39	1.67			
	PA4	8.59	5.11			
	PA5	6.12	2.41			
Yavaros		16.11	10.32	9.4	0.55	1.91
	YA1	4.1	2.45			
	YA2	2.67	2.65			
	YA3	1.97	1.46			
	YA4	2.37	1.47			
	YA5	4.99	2.29			

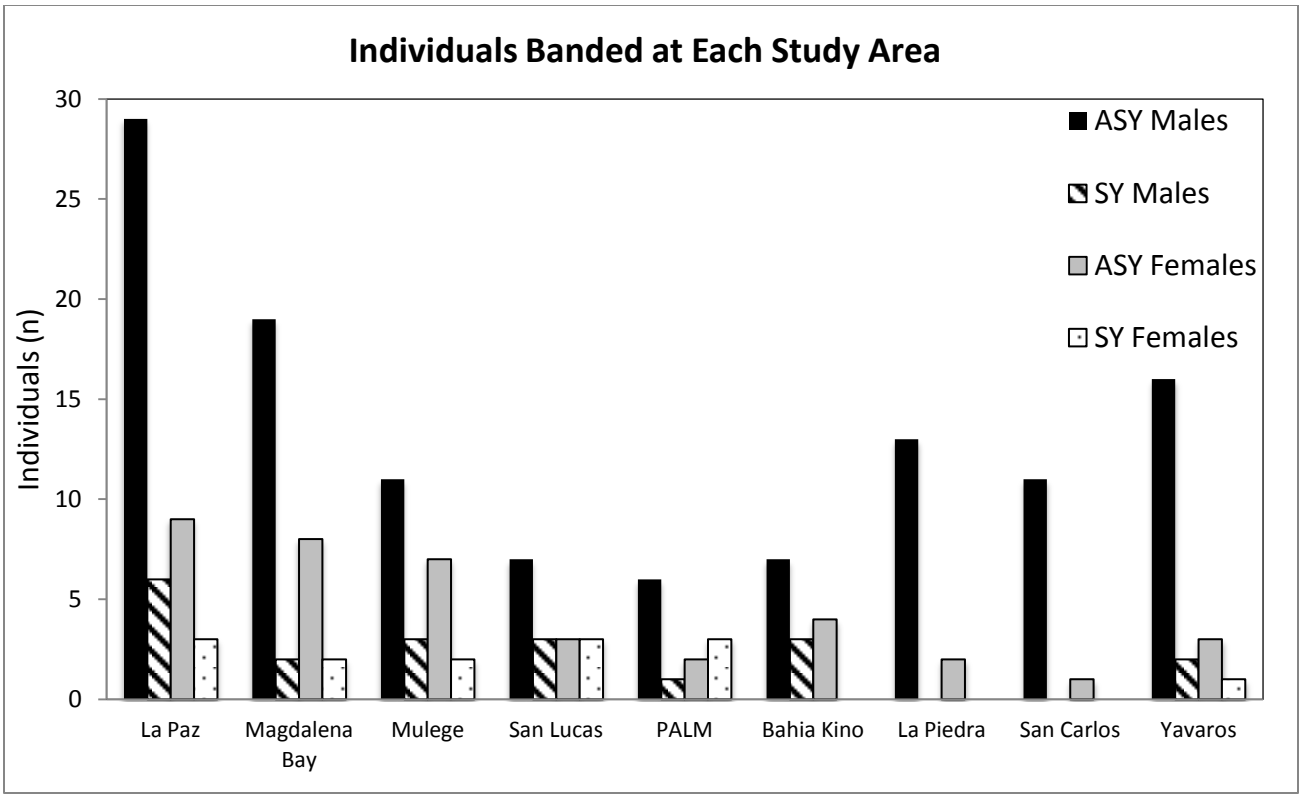

Fig. 12. Individuals banded at each study area divided by age class (after second year, ASY; second year, SY). Individuals from La Paz, Magdalena Bay, Mulegé, San Lucas and Puerto Adolfo López Mateos (PALM) study areas belong to *S. p. castaneiceps*. Individuals from Bahia Kino, La Piedra, San Carlos and Yavaros study areas are *S. p. rhizophorae*.

Table 2. MANOVA table comparing morphometric measurements among subspecies (*S. p. castaneiceps and S. p. rhizophorae*), sex (male and female), and the interaction of subspecies and sex.

	dF	Pillai	Approx. F	Num. dF	Den. dF	P
Subspecies	1	0.72	63.91	7	178	<0.001
Sex	1	0.49	24.64	7	178	<0.001
Subspecies:Sex	1	0.02	0.55	7	178	0.79
Residuals	184					

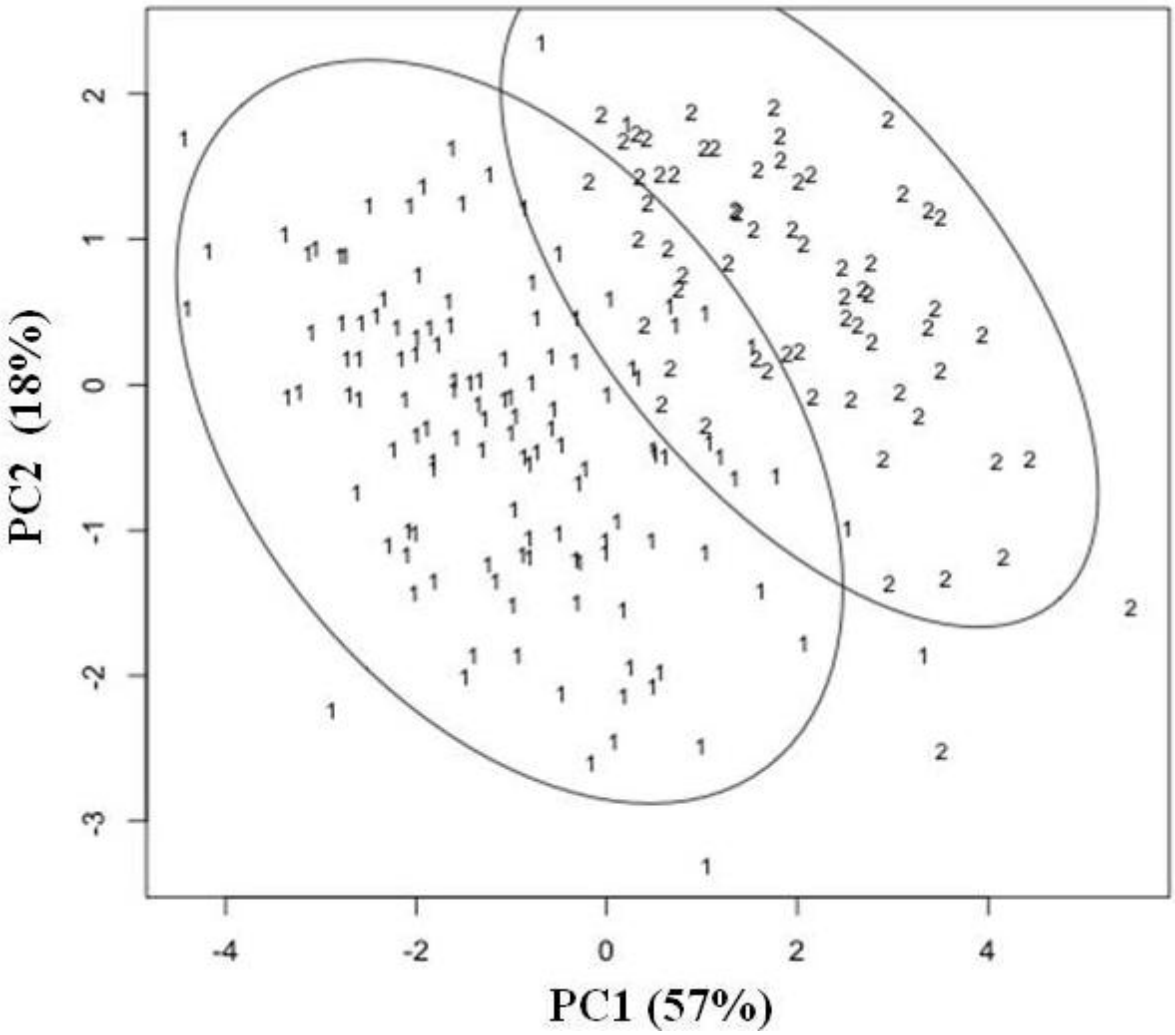

Fig. 13. Biplot of Principal Component Analysis (PCA) with 95% confidence ellipses. 1 refers to *S. p. castaneiceps* and 2 refers to *S. p. rhizophorae* individuals.

Table 3. Summary of biometrics measurements on each Mangrove Warbler subspecies separated by sex and age class. All measurements are averages in mm, except weight which is g. Standard deviation follows the averages ($\bar{x} \pm$s.d).with range in parentheses below.

Population	Sex	Age Class	n	Biometric Measurements						
				Wing Chord	Bill Length	Bill Depth	Tarsus Length	Tail Length	Total Length	Weight
S. p. castaneiceps			129	64.32±2.60 (57-69.5)	11.21±0.43 (9.8-12.2)	3.87±0.31 (3.1-4.5)	21.78±0.63 (20-24)	50.94±2.13 (45-55.3)	116.81±3.36 (110-127)	11.68±0.95 (8.3-14.2)
	Male		87	65.60±1.90 (60.5-69.5)	11.23±0.46 (9.8-12.2)	3.89±0.31 (3.1-4.5)	21.92±0.65 (20-24)	51.61±1.96 (48-55.3)	117.92±3.06 (110-127)	11.89±0.78 (10.1-14.1)
		ASY	72	66.13±1.45 (61.2-69.5)	11.24±0.41 (10.1-12.2)	3.88±0.31 (3.1-4.5)	21.94±0.66 (20-24)	51.94±1.92 (50.1-55.3)	118.31±2.96 (112-127)	11.99±0.78 (10.1-14.1)
		SY	15	63.07±1.85 (60.5-68)	11.19±0.67 (9.8-12.2)	3.92±0.27 (3.5-4.4)	21.79±0.59 (20.6-22.9)	50.03±1.32 (48-52)	116.07±2.93 (110-120)	11.45±0.59 (10.6-12.5)
	Female		42	61.61±1.64 (57-64.5)	11.18±0.37 (10.4-12)	3.82±0.31 (3.2-4.5)	21.50±0.48 (20.7-22.7)	49.51±1.74 (45-53)	114.45±1.74 (110-121)	11.22±1.12 (8.3-14.2)
		ASY	29	62.29±1.12 (60.5-64.5)	11.15±0.36 (10.4-12)	3.84±0.33 (3.3-4.5)	21.51±0.49 (20.8-22.7)	50.02±1.43 (47-53)	115.32±2.50 (110.8-121)	11.26±1.20 (8.3-14.2)
		SY	13	60.15±1.66 (57-63)	11.25±0.40 (10.4-11.9)	3.75±0.28 (3.2-4.1)	21.48±0.49 (20.7-22.1)	48.28±1.87 (45-52)	112.34±1.98 (110-116)	11.14±0.94 (9.9-13)
S. p. rhizophorae			63	62.37±2.27 (56.2-66)	10.40±0.47 (9.2-11.3)	3.25±0.16 (2.9-3.8)	20.76±0.58 (19.8-21.8)	49.98±2.01 (44.8-53)	112.0±3.44 (103-119)	10.02±0.71 (8.3-11.7)
	Male		52	63.1±1.63 (59-66)	10.41±0.46 (9.2-11.3)	3.25±0.16 (2.9-3.8)	20.83±0.59 (19.8-21.8)	50.51±1.57 (46-53)	112.75±2.80 (106.3-119)	10.13±0.66 (8.3-11.7)
		ASY	47	63.07±1.44 (59-66)	10.46±0.42 (9.2-11.3)	3.26±0.16 (2.9-3.8)	20.95±0.54 (19.8-21.8)	50.57±1.78 (46-53)	112.61±2.75 (106.3-119)	10.27±0.58 (8.3-11.4)
		SY	5	61.12±2.19 (59-64.5)	10.26±0.32 (10-10.8)	3.18±0.08 (3.1-3.3)	20.62±0.85 (19.8-21.8)	50.0±1.51 (48.6-52.5)	111.56±3.20 (109-117.1)	10.12±0.99 (9-11.7)
	Female		11	58.91±1.56 (56.2-61.9)	10.32±0.51 (9.3-11.2)	3.28±0.21 (3-3.8)	20.45±0.44 (20-21.2)	47.23±1.82 (44.8-50)	108.09±3.92 (103-116)	9.51±0.72 (8.4-11)
		ASY	10	58.97±1.63 (56.2-61.9)	10.23±0.44 (9.3-10.8)	3.3±0.21 (3-3.8)	20.37±0.38 (20-21)	47.24±1.93 (44.8-50)	107.99±4.15 (103-116)	9.5±0.76 (8.4-11)
		SY	1	58.3	11.2	3.1	21.2	47.1	109	9.6
Overall			192	63.68±2.66 (56.2-69.5)	10.95±0.59 (9.2-12.2)	3.67±0.39 (2.9-4.5)	21.45±0.78 (19.8-24)	50.63±2.13 (44.8-55.3)	115.24±4.06 (103-127)	11.13±1.17 (8.3-14.2)
	Male		139	64.66±2.17 (59-69.5)	10.92±0.61 (9.2-12.2)	3.65±0.40 (2.9-4.5)	21.51±0.82 (19.8-24)	51.20±1.89 (46-55.3)	115.99±3.88 (106.3-127)	11.23±1.13 (8.3-14.1)
	Female		53	61.04±1.96 (56.2-64.5)	11.00±0.53 (9.3-12)	3.71±0.37 (3-4.5)	21.28±0.64 (20-22.7)	49.06±1.96 (44.8-53)	113.20±3.89 (103-121)	10.87±1.26 (8.3-14.2)

Table 4. Summary of variance explained by Principal Component Analysis (PCA) comparing biometrics of *S. p. castaneiceps* and *S. p. rhizophorae*.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Standard Deviation	1.99	1.11	0.72	0.68	0.6	0.51	0.46
Proportion of Variance	0.57	0.18	0.07	0.07	0.05	0.04	0.03
Cumulative Proportion	0.57	0.74	0.82	0.88	0.93	0.97	1.00

Table 5. Factor loading (correlation coefficients between factors and variables) of the Principal Component Analysis (PCA) of the seven morphological traits used to evaluate the biometric variation between Mangrove Warblers. Only the first two principal components are shown.

	Wing Chord	Bill Length	Bill Depth	Tarsus Length	Tail Length	Total Length	Weight
PC1	-0.80	-0.63	-0.70	-0.77	-0.63	-0.87	-0.83
PC2	0.41	-0.49	-0.49	-0.21	0.69	0.20	-0.14

Table 6. MANOVA table comparing morphometric measurements among study areas within subspecies. S.p.c=*Setophaga petechia castaneiceps*, S.p.r= *S. p. rhizophorae*.

	dF	Pillai	Approx. F	Num. dF	Den. dF	P
S.p.c by study area	5	0.52	1.95	35	595	0.001
Residuals	121					
S.p.r. by study area	3	0.81	2.97	21	168	<0.001
Residuals	60					

Table 7. ANOVA table comparing morphometric measurements among the five study areas (La Paz, Magdalena Bay, Puerto Adolfo López Mateos, Mulegé, and San Lucas) of *S. p. castaneiceps* in Baja California Sur, Mexico.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Wing Chord	4	36.73	9.18	1.36	0.25
Bill Length	4	2.87	0.72	4.14	<0.01
Bill Depth	4	0.31	0.08	0.77	0.55
Tarsus Length	4	4.10	1.02	2.76	0.03
Tail Length	4	36.24	9.06	1.96	0.10
Total Length	4	129.83	32.46	2.85	0.03
Weight	4	14.31	3.58	4.01	<0.01

Table 8. ANOVA post-hoc contrasts comparing bill length measurements among study areas of *S. p. castaneiceps*. The mean bill length of one study area was compared to the mean bill length of all other study areas. 1= La Paz, 2= Magdalena Bay, 3= Mulegé, 4=San Lucas, 5= Puerto Adolfo López Mateos (PALM), 2, 5= Magdalena Bay and PALM combined.

Contrast	DF	Contrast SS	Mean Square	F Value	Pr >F
1 vs. 2,3,4,5	1	0.88	0.88	5.09	0.03
2 vs. 1,3,4,5	1	0.31	0.31	1.82	0.18
3 vs. 1,2,4,5	1	0.04	0.04	0.26	0.61
4 vs. 1,2,3,5	1	1.35	1.35	7.78	<0.01
5 vs. 1,2,3,4	1	1.03	1.03	5.93	0.02
2,5 vs. 1,3,4	1	1.92	1.92	11.12	0.001

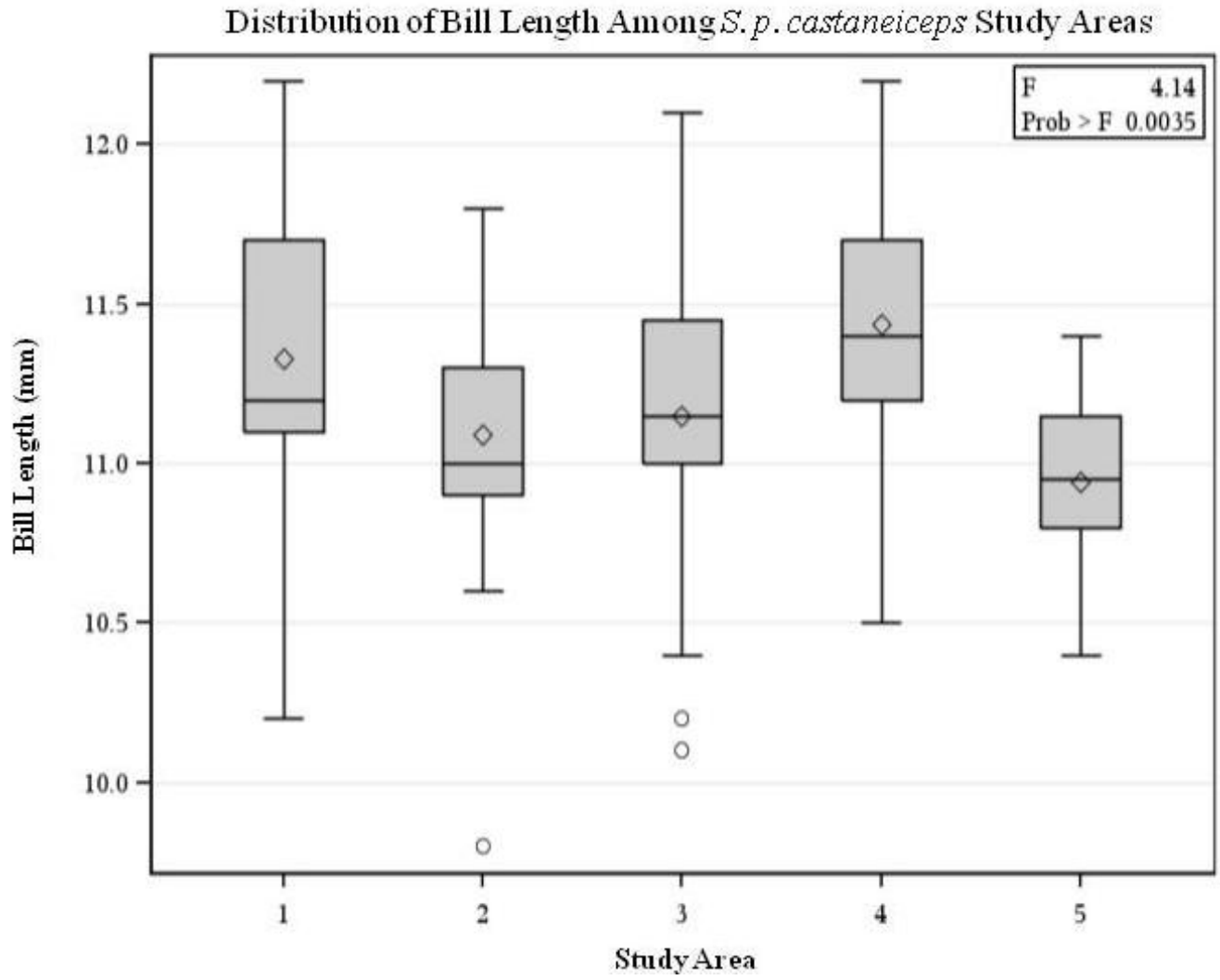

Fig. 14. Boxplot of bill lengths (mm) of *S. p. castaneiceps* among study areas in Baja California Sur, Mexico. 1= La Paz (n=47), 2= Magdalena Bay (n=27), 3= Mulegé (n=24), 4=San Lucas (n=17), and 5= Puerto Adolfo López Mateos (PALM) (n=12).

Table 9. ANOVA post-hoc contrasts comparing tarsus length measurements among study areas of *S. p. castaneiceps*. The mean tarsus length of one study area was compared to the mean tarsus length of all other study areas. 1= La Paz, 2= Magdalena Bay, 3= Mulegé, 4=San Lucas, 5= Puerto Adolfo López Mateos (PALM), 2, 5= Magdalena Bay and PALM combined.

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1 vs. 2,3,4,5	1	0.63	0.63	1.69	0.20
2 vs. 1,3,4,5	1	1.75	1.75	4.73	0.03
3 vs. 1,2,4,5	1	0.59	0.59	1.60	0.21
4 vs. 1,2,3,5	1	1.96	1.96	5.30	0.02
5 vs. 1,2,3,4	1	0.12	0.12	0.33	0.57
2,5 vs. 1,3,4	1	1.65	1.65	4.46	0.04

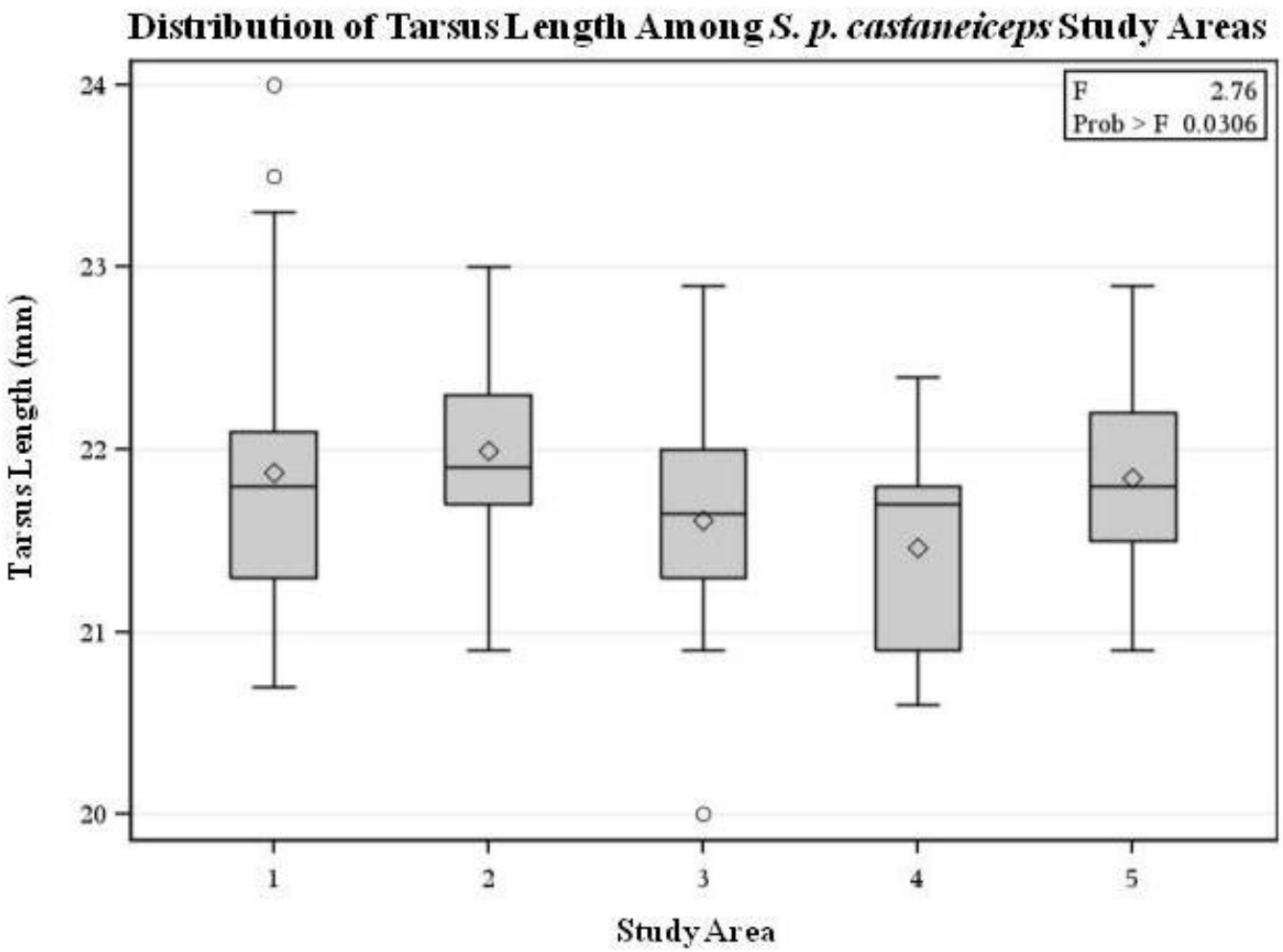

Fig. 15. Boxplot of tarsus lengths (mm) of *S. p. castaneiceps* among study areas in Baja California Sur, Mexico. 1= La Paz (n=47), 2= Magdalena Bay (n=27), 3= Mulegé (n=24), 4=San Lucas (n=17), and 5= Puerto Adolfo López Mateos (PALM) (n=12).

Table 10. ANOVA post-hoc contrasts comparing tail length measurements among study areas of *S. p. castaneiceps*. The mean tail length of one study area was compared to the mean tail length of all other study areas. 1= La Paz, 2= Magdalena Bay, 3= Mulegé, 4=San Lucas, 5= Puerto Adolfo López Mateos (PALM), 2, 5= Magdalena Bay and PALM combined.

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1 vs. 2,3,4,5	1	0.34	0.34	0.07	0.79
2 vs. 1,3,4,5	1	34.56	34.56	7.48	<0.01
3 vs. 1,2,4,5	1	2.03	2.03	0.44	0.51
4 vs. 1,2,3,5	1	5.70	5.70	1.23	0.27
5 vs. 1,2,3,4	1	0.61	0.61	0.13	0.72
2,5 vs. 1,3,4	1	11.76	11.76	2.55	0.11

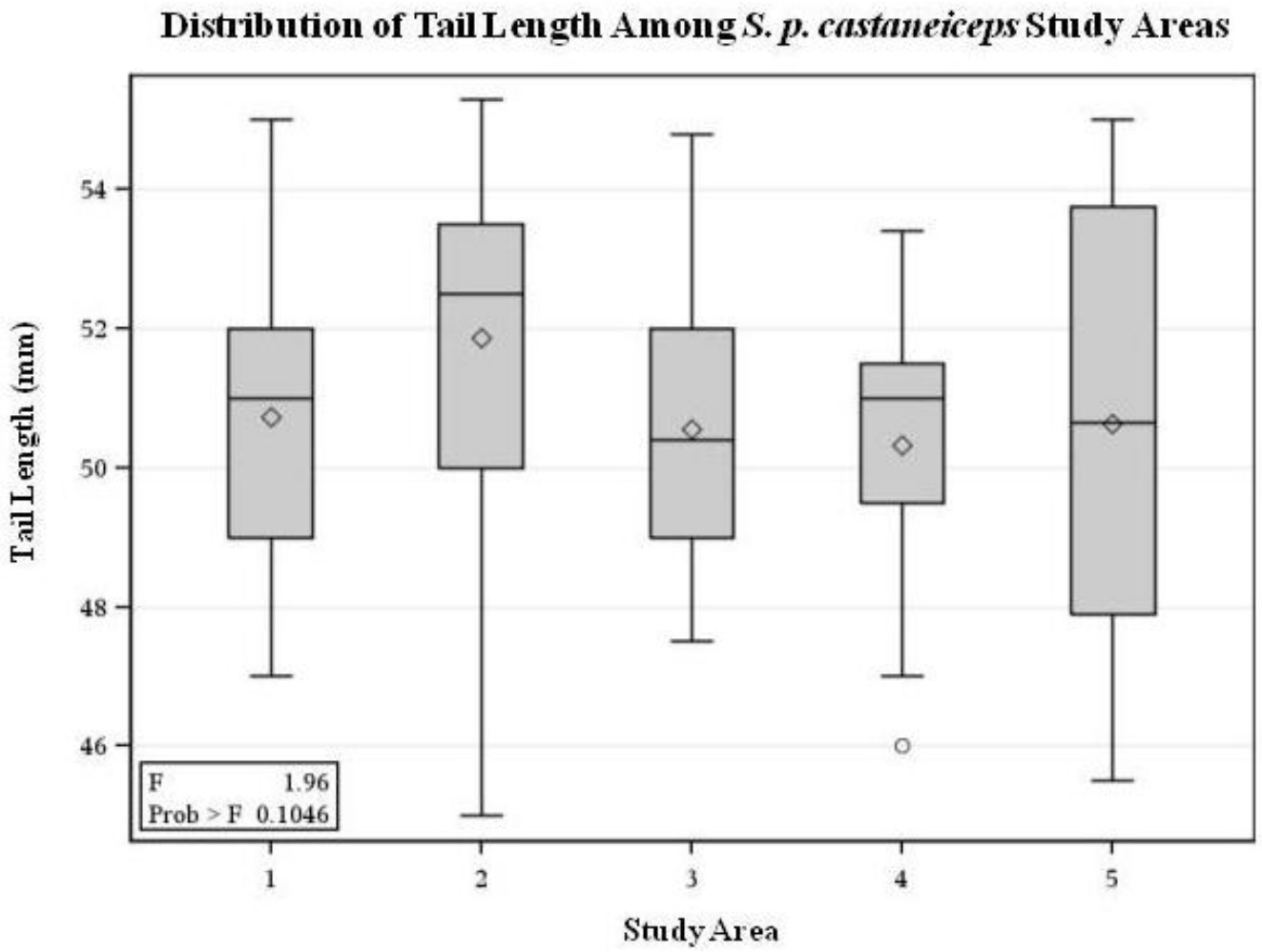

Fig. 16. Boxplot of tail lengths (mm) of *S. p. castaneiceps* among study areas in Baja California Sur, Mexico. 1= La Paz (n=47), 2= Magdalena Bay (n=27), 3= Mulegé (n=24), 4=San Lucas (n=17), and 5= Puerto Adolfo López Mateos (PALM) (n=12).

Table 11. ANOVA post-hoc contrasts comparing total length measurements among study areas of *S. p. castaneiceps*. The mean total length of one study area was compared to the mean total length of all other study areas. 1= La Paz, 2= Magdalena Bay, 3= Mulegé, 4=San Lucas, 5= Puerto Adolfo López Mateos (PALM), 2, 5= Magdalena Bay and PALM combined.

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1 vs. 2,3,4,5	1	29.28	29.28	2.57	0.11
2 vs. 1,3,4,5	1	84.78	84.78	7.45	<0.01
3 vs. 1,2,4,5	1	22.53	22.53	1.98	0.16
4 vs. 1,2,3,5	1	6.71	6.71	0.59	0.44
5 vs. 1,2,3,4	1	6.02	6.02	0.53	0.47
2,5 vs. 1,3,4	1	80.16	80.16	7.04	<0.01

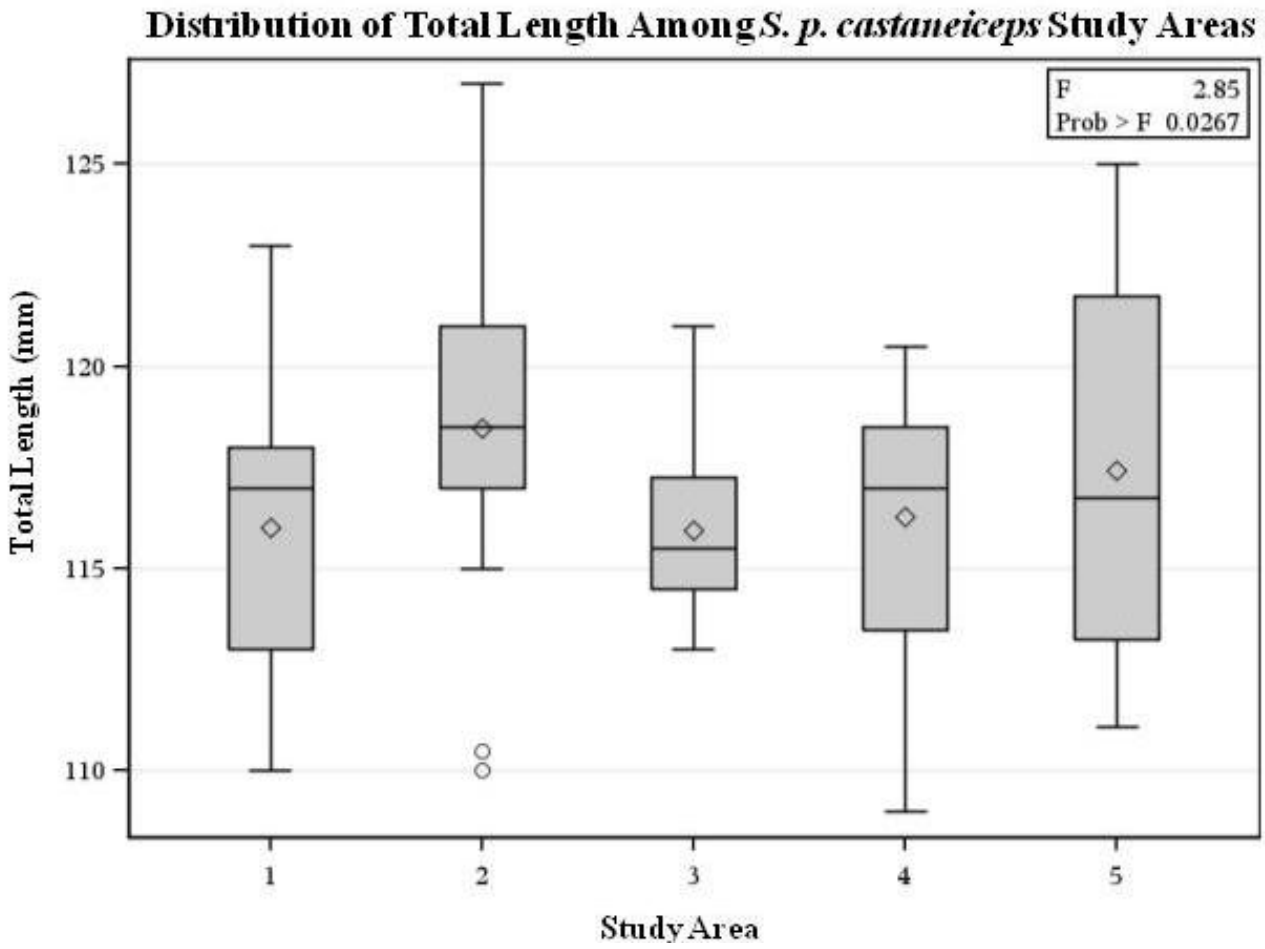

Fig. 17. Boxplot of total lengths (mm) of *S. p. castaneiceps* among study areas in Baja California Sur, Mexico. 1= La Paz (n=47), 2= Magdalena Bay (n=27), 3= Mulegé (n=24), 4=San Lucas (n=17), and 5= Puerto Adolfo López Mateos (PALM) (n=12).

Table 12. ANOVA post-hoc contrasts comparing weight measurements among study areas of *S. p. castaneiceps*. The mean weight of one study area was compared to the mean weight of all other study areas. 1= La Paz, 2= Magdalena Bay, 3= Mulegé, 4=San Lucas, 5= Puerto Adolfo López Mateos (PALM), 2, 5= Magdalena Bay and PALM combined.

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1 vs. 2,3,4,5	1	10.54	10.54	11.82	<0.001
2 vs. 1,3,4,5	1	2.82	2.82	3.16	0.08
3 vs. 1,2,4,5	1	0.25	0.25	0.28	0.60
4 vs. 1,2,3,5	1	0.31	0.31	0.35	0.56
5 vs. 1,2,3,4	1	2.66	2.66	2.98	0.09
2,5 vs. 1,3,4	1	7.76	7.76	8.70	<0.01

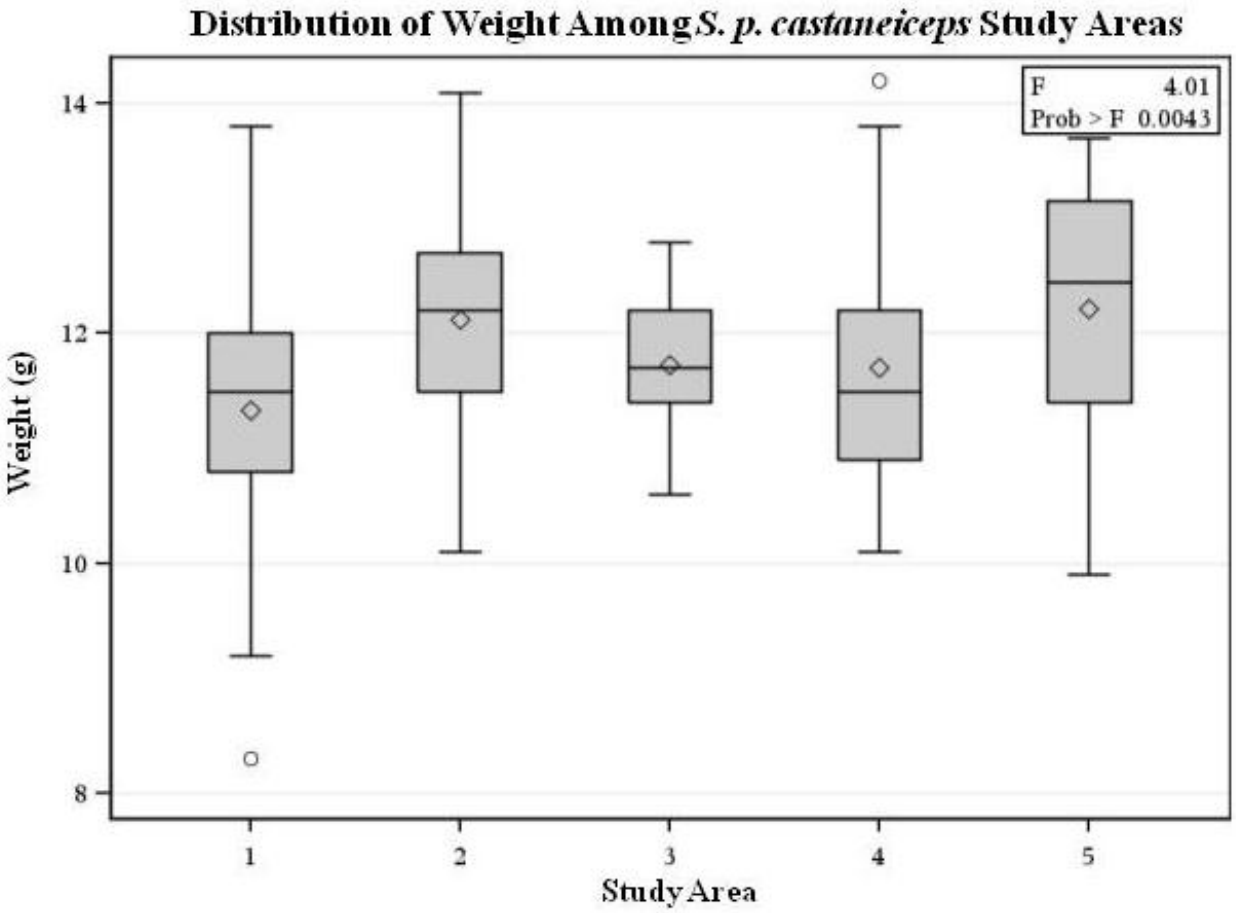

Fig. 18. Boxplot of weight (g) of *S. p. castaneiceps* among study areas in Baja California Sur, Mexico. 1= La Paz (n=47), 2= Magdalena Bay (n=27), 3= Mulegé (n=24), 4=San Lucas (n=17), and 5= Puerto Adolfo López Mateos (PALM) (n=12).

Table 13. ANOVA table comparing morphometric measurements among the four study areas (Bahia Kino, Yavaros, San Carlos, and La Piedra) of *S. p. rhizophorae* in Sonora, Mexico.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Wing Chord	3	75.10	25.03	6.13	<0.01
Bill Length	3	0.15	0.05	0.22	0.88
Bill Depth	3	0.02	0.01	0.26	0.85
Tarsus Length	3	2.03	0.68	2.07	0.11
Tail Length	3	68.34	22.78	7.80	<0.001
Total Length	3	200.40	66.80	7.58	<0.001
Weight	3	5.63	1.88	4.02	0.01

Table 14. ANOVA post-hoc contrasts comparing wing chord measurements among study areas of *S. p. rhizophorae*. The mean wing chord of one study area was compared to the mean wing chord of all other study areas. 1= San Carlos, 2= Bahia Kino, 3= La Piedra, 4=Yavaros.

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1 vs. 2,3,4	1	33.00	33.00	8.08	<0.01
2 vs. 1,3,4	1	68.75	68.75	16.84	<0.001
3 vs. 1,2,4	1	1.46	1.46	0.36	0.55
4 vs. 1,2,3	1	1.06	1.06	0.26	0.61

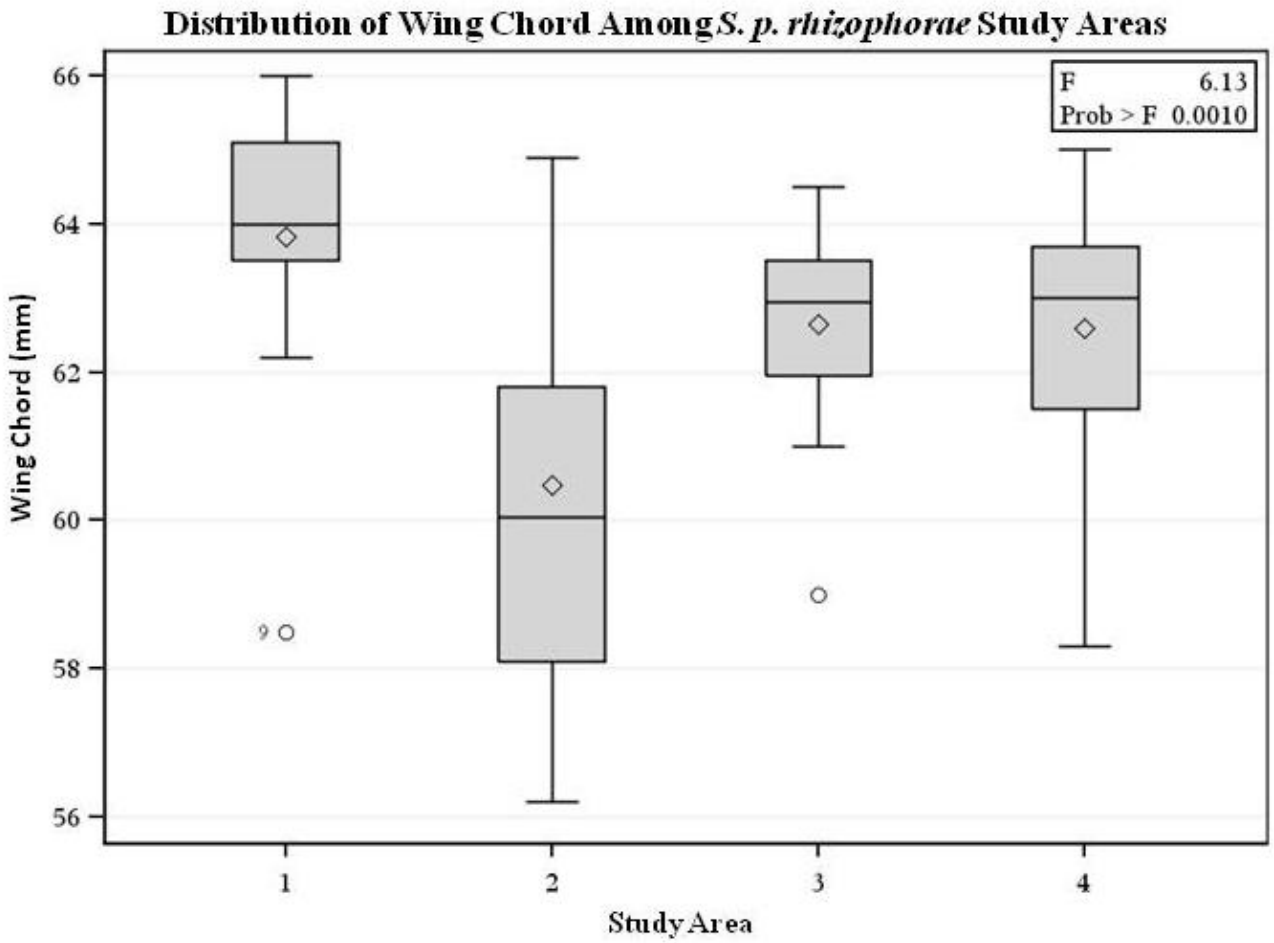

Fig. 19. Boxplot of wing chord (mm) of *S. p. rhizophorae* among study areas in Sonora, Mexico. 1= San Carlos (n=11), 2= Bahia Kino (n=14), 3= La Piedra (n=16), 4= Yavaros (n=23).

Table 15. ANOVA post-hoc contrasts comparing tarsus length measurements among study areas of *S. p. rhizophorae*. The mean tarsus length of one study area was compared to the mean tarsus length of all other study areas. 1= San Carlos, 2= Bahia Kino, 3= La Piedra, 4=Yavaros.

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1 vs. 2,3,4	1	0.04	0.04	0.11	0.74
2 vs. 1,3,4	1	0.16	0.16	0.49	0.49
3 vs. 1,2,4	1	0.37	0.37	1.12	0.29
4 vs. 1,2,3	1	1.91	1.91	5.84	0.02

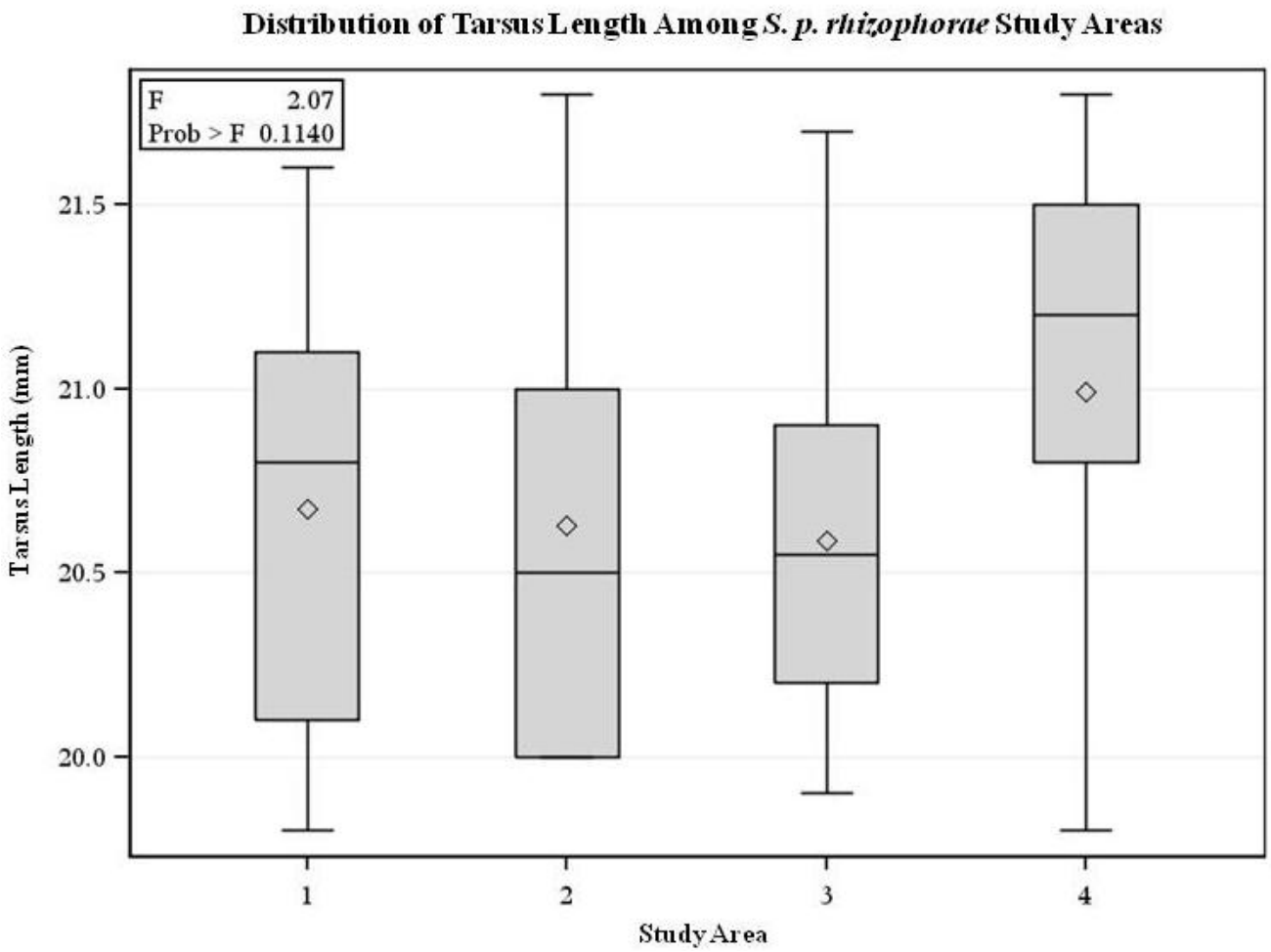

Fig. 20. Boxplot of tarsus length (mm) of *S. p. rhizophorae* among study areas in Sonora, Mexico. 1= San Carlos (n=11), 2= Bahia Kino (n=14), 3= La Piedra (n=16), 4= Yavaros (n=23).

Table 16. ANOVA post-hoc contrasts comparing tail length measurements among study areas of *S. p. rhizophorae*. The mean tail length of one study area was compared to the mean tail length of all other study areas. 1= San Carlos, 2= Bahia Kino, 3= La Piedra, 4=Yavaros.

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1 vs. 2,3,4	1	10.54	10.54	3.61	0.06
2 vs. 1,3,4	1	66.72	66.72	22.85	<.0001
3 vs. 1,2,4	1	3.58	3.58	1.22	0.27
4 vs. 1,2,3	1	10.87	10.87	3.72	0.06

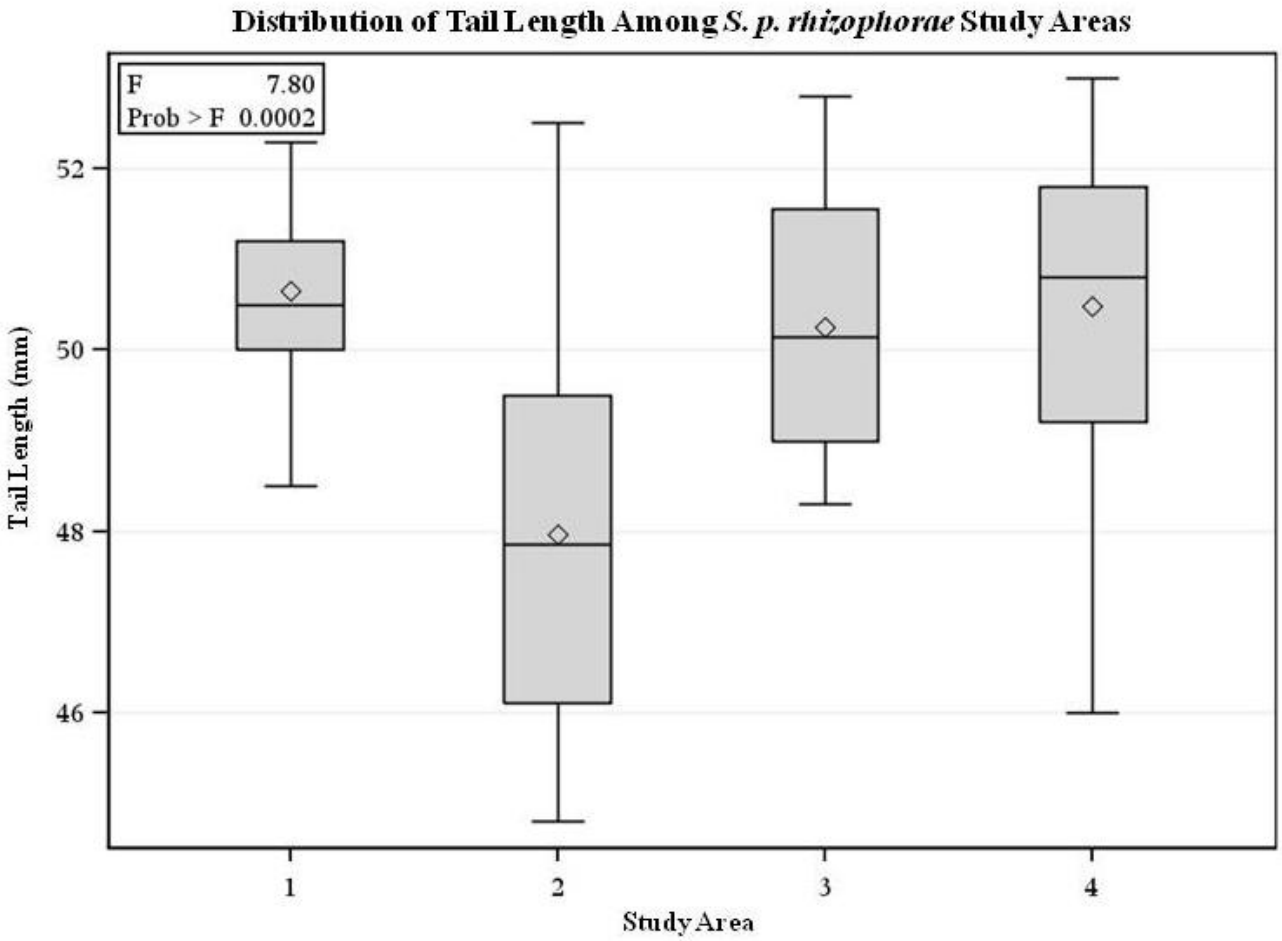

Fig. 21. Boxplot of tail length (mm) of *S. p. rhizophorae* among study areas in Sonora, Mexico. 1= San Carlos (n=11), 2= Bahia Kino (n=14), 3= La Piedra (n=16), 4= Yavaros (n=23).

Table 17. ANOVA post-hoc contrasts comparing total length measurements among study areas of *S. p. rhizophorae*. The mean total length of one study area was compared to the mean total length of all other study areas. 1= San Carlos, 2= Bahia Kino, 3= La Piedra, 4=Yavaros.

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1 vs. 2,3,4	1	107.95	107.95	12.25	<0.001
2 vs. 1,3,4	1	164.62	164.62	18.69	<.0001
3 vs. 1,2,4	1	7.10	7.10	0.81	0.37
4 vs. 1,2,3	1	1.45	1.45	0.16	0.69

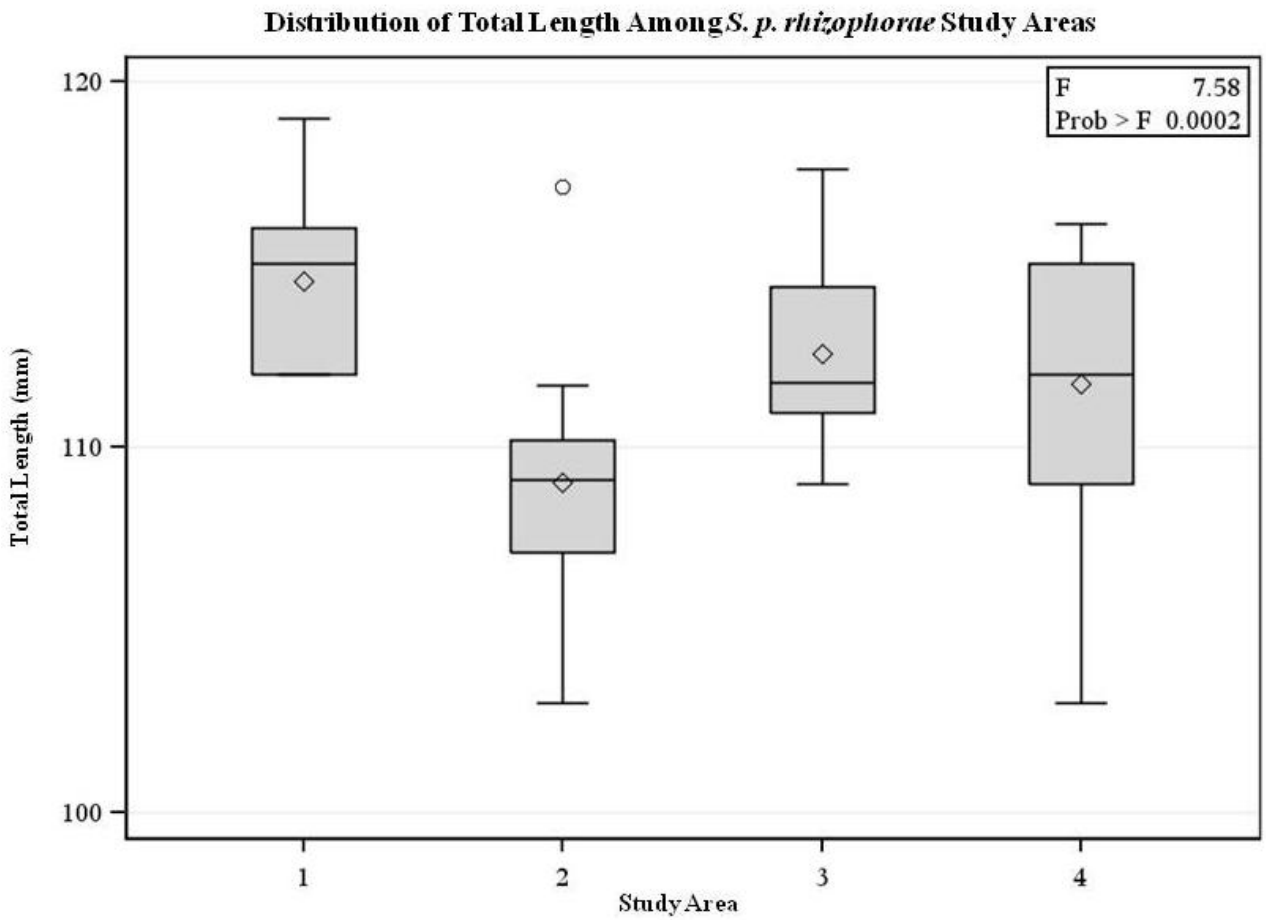

Fig. 22. Boxplot of total length (mm) of *S. p. rhizophorae* among study areas in Sonora, Mexico. 1= San Carlos (n=11), 2= Bahia Kino (n=14), 3= La Piedra (n=16), 4= Yavaros (n=23).

Table 18. ANOVA post-hoc contrasts comparing weight measurements among study areas of *S. p. rhizophorae*. The mean weight of one study area was compared to the mean weight of all other study areas. 1= San Carlos, 2= Bahia Kino, 3= La Piedra, 4=Yavaros.

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1 vs. 2,3,4	1	0.24	0.24	0.51	0.48
2 vs. 1,3,4	1	0.01	0.01	0.01	0.91
3 vs. 1,2,4	1	2.07	2.07	4.43	0.04
4 vs. 1,2,3	1	4.59	4.59	9.84	<0.01

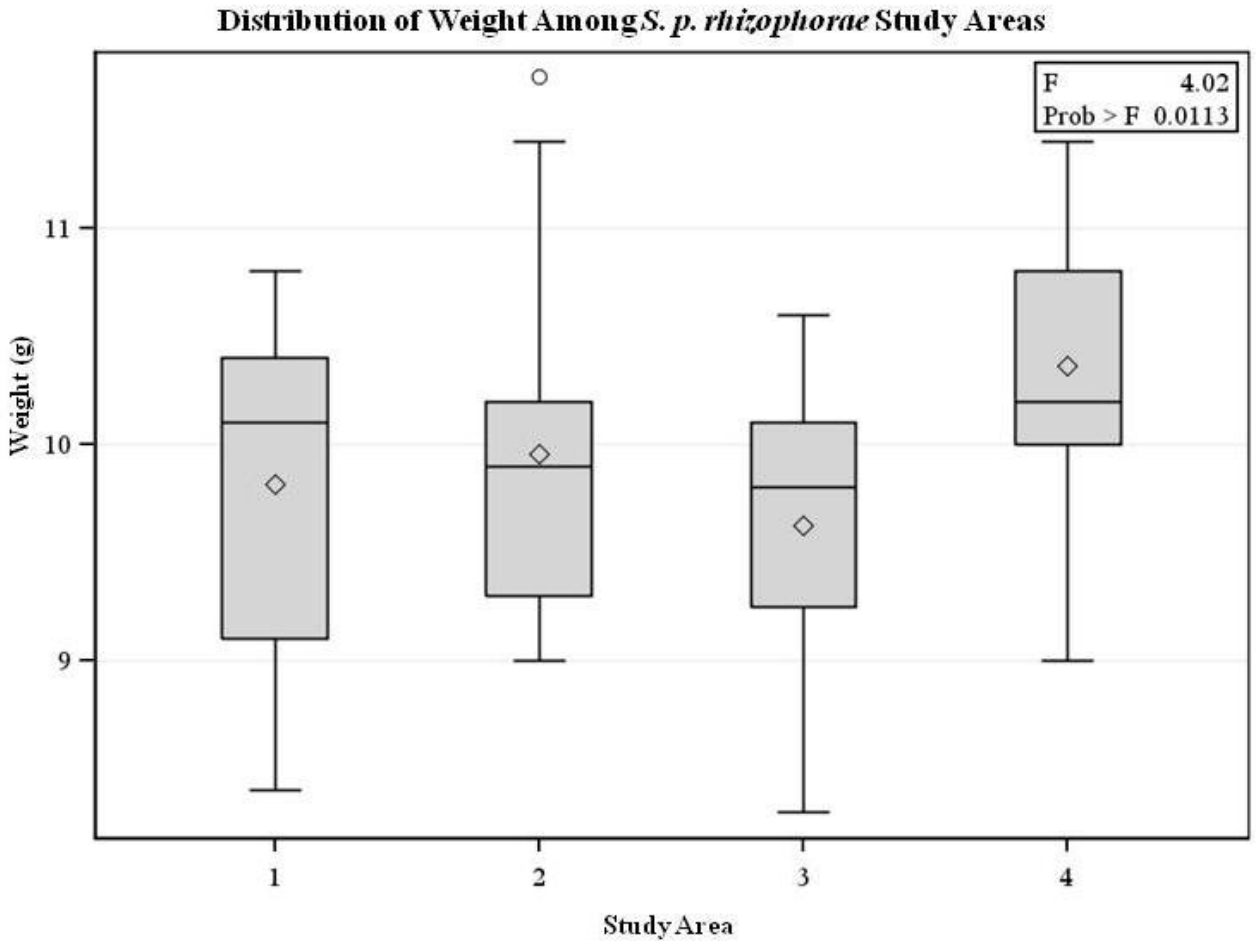

Fig. 23. Boxplot of weight (g) of *S. p. rhizophorae* among study areas in Sonora, Mexico. 1= San Carlos (n=11), 2= Bahia Kino (n=14), 3= La Piedra (n=16), 4= Yavaros (n=23).

CHAPTER III

YEAR ROUND MOVEMENTS OF A MANGROVE WARBLER SUBSPECIES *SETOPHAGA PETECHIA CASTANEICEPS* IN NORTHWESTERN MEXICO

INTRODUCTION

The underlying framework for the conservation of fragmented populations is founded on the principles of island biogeography (MacArthur and Wilson 1967), wherein the probability of species occurrence in habitat patches varies as a function of patch size and isolation (Prugh et al. 2008). Simberloff (1974) stated, "Any patch of habitat isolated from similar habitat by different, relatively inhospitable terrain traversed only with difficulty by organisms of the habitat patch may be considered an island." Habitat islands are exposed to extinction through demographic stochasticity, environmental stochasticity, loss in genetic heterozygosity, edge effects, cultural erosion, and anthropogenic disturbance (Burkey 1995; Ludwig 1996). Rates of habitat fragmentation are so high that virtually all natural (continuous) terrestrial habitats and protected areas (such as nature preserves and parks) are certain to become habitat islands (Groombridge and Jenkins 2002).

The mangrove forest of Baja California Sur, Mexico is a mosaic of small islands as a result of habitat fragmentation due to increased pressures from human activities. Within twenty years (1972-92), 65% of mangrove forests in Mexico were destroyed due to anthropogenic disturbance (Herrera-Silveira and Ceballos-Cambranis 2000), 70,000 ha lost between 1993 and 2000 (SEMARNAT 2003) (including 2,300 ha across Northwestern Mexico (early 1970's to 2005) (Ruiz-Luna et al. 2010)), and over 50% of mangroves have been destroyed worldwide (Holguin et al. 2006). Furthermore, this region is affected by seasonal hurricanes which cause considerable damage on mangrove forests by reducing overall stem density and basal area and uprooting trees (Kovac et al. 2001). Not only are tropical depressions common, but 78% of the national total of hurricanes occur here (Flores-Verdugo et al. 1992). These influences combined with these weakened mangrove stands (e.g. those exhibiting homogeneous tree structure and

diversity, gaps or breaks in continuous vegetation, and poor health from lack of microbial benthic communities) in this area, present a great concern to study these unique habitats and preserve their biodiversity.

Few birds specialize in mangrove forests, and detailed research of the ecology of confined mangrove birds is sparse (Hogarth 1999; Luther and Greenberg 2009). The Mangrove Warbler (*Setophaga petechia castaneiceps*) is an insectivorous passerine endemic to the mangroves of Baja California Sur. It is one of 43 recognized subspecies of the Yellow Warbler (Browning 1994), and believed to be a sedentary (although no published data have confirmed this), habitat specialist confined to the use of mangroves year round (Curson et al. 1994). Resident tropical birds occupy a relatively constant environment where periods of extreme cold and severe winter weather conditions are absent. Although these areas experience fluctuations in precipitation (i.e. dry and rainy seasons), the lack of extreme seasonality is a major driving force behind the ability of tropical birds to maintain year-long territories often with monogamous pair bonds (Cox 1968). As suitable mangrove habitat is declining, mangrove birds are forced into diminutive, isolated patches along the coastline leading to exposure to the dynamics of small, island populations.

Despite low human density in this area, there is increasing pressure on mangrove stands from anthropogenic activities (e.g. shrimp farming, rice cultivation, and urban development) which has led to localized destruction and fragmentation (Páez-Osuna et al. 2003; Brusca 2004; Glenn et al. 2006). Mangrove forests, and resultantly their inhabitants, may also be subject to more disturbance than other forests due to their exposure to typhoons, coastal erosion, and fluctuating river discharges (Hogarth 1999; Luther and Greenberg 2009).

Considering the Mangrove Warbler specializes on a unique declining habitat, more research needs to be conducted to examine their movement patterns. Knowledge of their population movements will provide insight to immigration and emigration between mangrove stands, which is important for determining the susceptibility of the subspecies to consequences felt by isolated, small populations. Although the overall population size of *S. p. castaneiceps* is not known, it is reasonable to believe not many birds can be living in one patch due to the lack of available space and competition for resources such as nesting sites and food (e. g. Holmes 2010). Low individual numbers coupled with isolation and a sedentary lifestyle (possibly no immigration and emigration), may be resulting in low genetic variation (Harrison and Hastings 1996; Callens et al. 2011). There may be a high occurrence of inbreeding, thus leaving the populations more susceptible to environmental changes. Founder effects, or a bottle neck effect may have recently occurred due to hurricanes (e. g. five named hurricanes crossed Baja California Sur between 2001 and 2009; NOAA 2011) displacing individuals and destroying habitat, adding to genetic complications. Also, increased pressures from fragmentation may be felt by this subspecies due to the possible sensitivity to edge effect. Environmental stochasticity and catastrophes from living in coastal mangroves, in addition to the strengthened pressure of demographic stochasticity in their small populations may leave the viability of this subspecies uncertain and threatened with extinction.

OBJECTIVE

The main objective of this study was to quantify local movement of a presumed sedentary bird, *S. p. castaneiceps*.

HYPOTHESIS

I hypothesize these birds are truly sedentary, moving only throughout localized mangrove stands. I believe the adult males are extremely territorial and defend their territory year round.

Ho: *S. p. castaneiceps* will show movement between mangrove stands throughout their breeding range.

Ha: *S. p. castaneiceps* will not move between mangrove stands throughout their breeding range.

I expect to find birds (adult males and females) inhabiting small patches in the Baja California Sur study sites, to be present year round in the mangrove stands in which they breed with no movement to surrounding mangrove stands that are separated by inhospitable habitat.

STUDY AREA

The study area included the known range of *S. p. castaneiceps*. *S. p. castaneiceps* inhabits patches of mangroves from both coasts of central Baja California Sur from San Ignacio and Pond lagoons south to about 27°N on the Gulf of California (Browning 1994; Dunn and Garrett 1994).

Baja California Sur has an annual precipitation <300 mm and mean temperatures of 20-22°C classifying this as an arid climate (Ruiz-Luna et al. 2010). Mangroves in this study area are represented by three species, *Avicennia germinans* (black mangrove), *Rhizophora mangle* (red mangrove), and *Laguncularia racemosa* (white mangrove) (Hogarth 1999; Flores-Verdugo et al. 1992; Ruiz-Luna et al. 2010). Mangrove trees in Baja California Sur seldom exceed 5 m in height, unlike other tropical areas (Felger et al. 2001). Although there are no consistent patterns

in species distribution or assemblage structure of mangroves in Mexico (Ruiz-Luna et al. 2010), study areas in Baja California Sur were dominated by red mangrove.

I placed 16 study sites in Baja California Sur based on locations reported in Whitmore et al. (2000) within 5 major study areas: La Paz, Magdalena Bay, Puerto Adolfo López Mateos (hereafter referred to as PALM), Mulegé and San Lucas (Fig. 1-6). Thirteen sites were situated on the Sea of Cortez coastline. Each study site was designated as a mangrove stand separated by inhospitable habitat from the next closest stand.

All study sites on the Sea of Cortez were less than 1.8 km (straight line distance) across at greatest distance (length or width) and were isolated patches separate from each other. All but one study site (LP6) on the Sea of Cortez coast were <6 ha in total area (Table 1). Magdalena Bay is a large continuous mangrove stand on the Pacific Coast of Baja California Sur. It stretches (straight line distance) approximately 115 km along the coast. The Magdalena Bay study area had the greatest total area (67.8ha). The entire study area spanned a total straight line distance of 390 km and cumulative total area of 127.5ha. The overall average distance between neighboring study sites was 6.6 km, but ranged from 0.91km to 31.8km (Table 1).

METHODS AND MATERIALS

Data Collection

I captured and banded Mangrove Warblers during the breeding season (March-July 2010) at each study site in Baja California Sur using mist nets and playback recordings of their songs as a decoy. General behavior was recorded for all observed individuals during the playback to determine territoriality. A male, female, or pair was considered to be actively defending a territory when exhibiting wing flutters, flying at the speaker or observer, chipping, chasing other

birds, or counter-singing to playback. Within any study site, multiple locations (i.e. net lanes) were used to conduct necessary field work. As many individuals as possible were captured to maximize sample size.

Each bird was banded with a U.S. Geological Service aluminum band and unique color combination (4 color plastic bands) for individual identification (Permit # 20580). The leg containing the federal band was marked with a color band corresponding to one of the five major study areas (La Paz, Magdalena Bay, PALM, Mulegé, and San Lucas). The other leg was marked with three color bands. At the time of capture, all locations were recorded via GPS unit with a minimum of 10 m accuracy. After processing, birds were released at point of capture.

Age was determined through plumage and skull pneumatization (Howell and Webb 1995; Pyle 1997). Birds were categorized into hatch year (HY) and after hatch year (AHY) year classes. Sex, male (M) or female (F), was determined through coloration and presence of brood patch/cloacal protuberance (Howell and Webb 1995; Pyle 1997). All individuals that were not capable of being sexed were classified as unknown (U). Skull pneumatization was based on a 0-6 scale, where 0 indicates no ossification and 6 indicates full ossification of the skull. A class 6 skull indicates an AHY individual. A pair was recorded if both a female and male were captured at the same location and defended the territory together.

As reported by Salgado- Ortiz et al. (2008), *D. p. bryanti* in Celestun, Mexico defended territories and maintained permanent pair bonds and stable population density year round. Since I was interested in year round movements within the *S. p. castaneiceps* population(s), banded adult males and females were re-trapped and/or re-sighted throughout differing periods of the year (Morton and Stuchbury 2000). Adult Mangrove Warblers in Baja California Sur were re-sighted/re-trapped in late fall/early winter (November 2010) and breeding season (April 2011).

The November 2010 re-sighting period is the wintering re-sighting period and April 2011 is referred to as the breeding re-sighting period. This re-sight schedule allowed for a year round observation of a presumed sedentary bird.

Re-sighting and re-trapping both took place at points of original capture (net locations). Each point of original capture was visited at least once within the differing periods as described above. At each location, I broadcasted conspecific vocalizations to call individuals to the area. Broadcasts were played for 15 minutes or until an individual (banded or unbanded) was seen or heard. All detected (observed and heard) individuals of all ages and sexes were recorded during the 15 minute time period within a 10 m radius surrounding the point (Hutto et al. 1986). General behavioral notes also were collected during re-sighting attempts. I chose a small radius due to the density of the vegetation and to ensure 100% detection. More time was spent at the re-sighting location if band confirmation was needed, however no individuals were recorded after the 15 minute survey.

If re-trapping was used, all individuals were target netted with mist nets after the 15 minute re-sighting period. I re-trapped mangrove warblers if they were un-banded, to assess the condition of their bands, replace missing color bands, or needed to confirm band combination (of previously banded individuals). I found the color bands faded throughout the year due to high exposure to sun and salt. Captured unmarked individuals were banded, measured, and released.

To standardize re-sighting efforts, net hours and observation hours were recorded to keep effort as equal as possible (Winker et al. 1997) per original capture location. They also occurred during the same time periods of the day of original capture and under desirable field conditions, with slight differences due to yearly changes in sunrise/sunset times. By standardizing re-sight efforts by original capture location (regardless of how many birds were captured at that location)

I attempted to keep the distance the broadcasts could be heard equal, thus reducing the amount of birds that may have been drawn in to the area of broadcast.

I followed methods for recording re-sights of banded bird data in SWCA Environmental Consultant's Southwestern Willow Flycatcher Re-sight Protocol (SWCA unpubl.). Observations (via 10X42 binoculars) were recorded noting the order and color of the bands on the respective legs, the location of the bird (via GPS waypoint), and confidence level for the observation. Re-sighting was recorded on an A, B, or C classification level. An 'A' confidence level consisted of an observation recorded at 100% confidence of the full band combination of both legs and it must be observed twice. A 'B' re-sight entailed a 100% confidence level of the full band combination on both legs, but it was only observed once. Any other observations of full band combinations or partial band combinations on only one or both legs were classified as a 'C' re-sight. To eliminate observer bias, no discussion of band combos was shared amongst observers.

Data Analyses

Only males and females captured during the 2010 breeding season were referred to as the banded population. Unless noted, I assumed all points of original capture during the 2010 breeding season were the active territories of the responding individuals due to territorial behavior. All individuals that could not be reliably sexed were excluded from analyses. Individuals that were detected multiple times during a re-sighting survey point were only counted once. If an individual followed the observers to a neighboring re-sighting point (which was obvious in the field), it was only counted once at the point where it actively defended a territory.

Re-sighting success was defined as the percent of re-sighted individuals from the total banded population during each re-sighting period. This was calculated by dividing the total number of re-sighted individuals by the total banded population and multiplying this number by 100 to achieve a percentage. Due to some study sites being visited more often than others throughout the breeding and non-breeding re-sighting periods, percent re-sighted individuals by effort was needed. Percent re-sighted individuals by effort were calculated by dividing total re-sighted individuals by total attempted re-sighted individuals. The total number of attempted re-sighted individuals was calculated by subtracting the total amount of birds with no re-sight effort from the total banded population. This number was then multiplied by 100 to obtain a percentage. Population density was calculated by dividing the number of individuals detected during the 15 minute surveys by respective area (ha) of study area, study site, and overall.

A repeated measures analysis of variance (ANOVA) was used to test for any significant differences among breeding (2010 and 2011) and wintering (2010) bird densities for all sex categories (male, female, and pair). This test was run using statistical software SAS (version 9.2). We checked the normality of the response variable density through graphical exploration (histograms and quantile-quantile plots) and Shapiro-Wilk normality tests. We learned the data were skewed to the right and required transformation to reduce the spread of the response variable and lead to a better approximation of normality to satisfy ANOVA test assumptions. We found the cube root transformation was the best transformation to the data to approximate normality.

The cube root transformed data were then used in SAS (version 9.2) in a mixed model repeated measures analysis of variance exploring three different covariance structures: Unstructured, Autoregressive (AR1), and Toeplitz. We selected the covariance structure that

best fit the data by means of several different criteria including Akaike Information Criterion (AIC), AIC corrected (AICc) and the Bayesian Information Criterion (BIC). We used the same predictor variables for these models, but the covariance structure between the repeated measures was best explained by the AR1 covariance structure in comparison to the other alternative covariance structures. A result was significant when $p < 0.05$.

The re-sight data were then used to determine individual movements throughout the year. I used ESRI ArcMap 9.3.1 to assess distances moved by banded individuals from their original capture location. I determined territory switching and territory replacement in individuals by confirming waypoints with re-sighting data and comparing this to previous confirmed locations of the individual. I calculated the closest straight line distance of movements using ESRI ArcMap 9.3.1 measure tool.

RESULTS

Capture, Territoriality, and Re-sighting Success

I captured and banded 74 adult males and 34 adult females (28 pairs; Fig. 7) during the 2010 breeding season at 57 capture locations within the 16 study sites. Every individual captured was actively defending its territory. Chipping was the main territorial cue used by Mangrove Warblers both in the wintering season and breeding season. Song was only secondary in defending their territory. Although minimal song was used in the morning (morning chorus) of the breeding season, it was infrequent and chip notes between birds were used more reliably to communicate. Playing song and chip notes during both re-sighting periods led to aggression in both the male and female territory holders in which they would chase off any (including migrant yellow warblers) intruding individuals. Adult male movement involved more flying and chasing

whereas female aggression was harsh chipping companied by hopping internally throughout the mangrove trees looking for the unrecognized individual.

I re-sighted 43 marked males and 13 marked females, obtaining a total re-sight success of 51.9% of the total banded population. Nine marked males and 2 marked females were re-sighted both in the spring and winter re-sighting periods. I re-sighted 4 retained pair bonds throughout the course of this study. The highest number of re-sighted marked birds (n=25) was in the La Paz study area, whereas the lowest (n=6) was in Magdalena Bay (Fig. 7). Mulegé study area had the greatest percent of re-sighted banded males (75.0%) and the greatest percent of re-sighted banded females (55.6% 0) (Table 2). Marked males had an overall re-sight success of 58.1% whereas females were 38.2% (Table 2). A higher percentage of males and females (37.3% (n=22) and 20.0% (n=5) respectively) were re-sighted during the winter period compared to the spring re-sighting period (29.7% and 14.29% respectively, Table 2).

Population Density

Density of adult males, adult females and pairs was highest in the San Lucas study area in the 2010 breeding season (2.2/ha, 1.7/ha, and 1.7/ha respectively) and 2010 wintering season (1.5/ha, 1.0/ha, and 1.0/ha respectively) (Table 3). The Mulegé study area had the highest density of males, females and pairs (1.1/ha) in the 2011 breeding season (Table 3). The overall average year-round adult male density was 1.3/ha, adult year-round female density 0.9/ha, and adult year-round pair density 0.9/ha. Males had a significantly higher density across all seasons (Breeding 2010, Wintering 2010, Breeding 2011) ($F=4.27$, $dF=132$, $P=0.02$) (Table 4) compared to females and pairs (Fig. 8). There was no significant change in overall Mangrove Warbler density across seasons (Table 4, Fig. 9).

Territory Switching

By comparing location of original capture versus location of re-sight, I detected no among patch movements throughout the *S. p. castaneiceps* population. Some banded adults, however, moved their territories to different locations (territory switching) within their study site between the breeding periods (2010-2011). All movements were recorded to occur between the wintering (2010) and breeding (2011) re-sighting periods. Movement of a territorial banded male to another territory was witnessed 8 times with an average distance of 0.59 km between locations (Table 5). Females were only found to move to a new territory once, which was to the closest neighboring territory with a male.

Territory Replacement

A territory became vacant 68 times during the study (Table 6). An open territory was filled by another male, hereafter called territory replacement, 68.1% (n=32 replacements of 47 vacancies) of the time. An opening in a female position was filled 66.7% (n=14 replacements of 21 vacancies) of the time it occurred. Unbanded males and females were more likely to fill vacant territories (n=25) than banded males and females (n=7, n=1, Table 6). Most re-sighted individuals from a pair bond were replaced in the absence of one individual (n=11). All but four of the territory replacements were noted during the breeding season (2011) re-sighting period**,** compared to the wintering (2010) re-sighting period

DISCUSSION

My results confirm the Mangrove Warbler, *S. p. castaneiceps,* is a resident tropical passerine of Baja California Sur, Mexico. The Mangrove Warbler has minimal seasonal

movements (both adult male and female) and was observed to actively defend its territory year round (pers. obs.), much like other tropical passerines (Greenberg and Gradwohl 1986, 1997; Lefebvre et al. 1992; Morton et al. 2000; Salgado-Ortiz et al. 2008). Although not all banded individuals were re-sighted and new unbanded adult mangrove warblers were witnessed in various mangrove sites during both re-sighting periods, it is plausible to believe *S. p. castaneiceps* is a sedentary species performing only post-juvenile movements. Lack of re-sighting success could be due to mortality, loss of bands, or missed detection. Lack of re-sighting success cannot be due to emigration of individuals from study sites because all mangrove stands in Baja California Sur were surveyed. The unbanded adults may have been present but missed during original (2010 breeding) surveys due to lack of territorial behavior. Mangrove stands are densely vegetated (Hernández et al. 2011) making it difficult to see Mangrove Warblers. Furthermore, no movement from original mangrove sites were recorded in any re-sighted individual.

Despite high replacement of individuals in these patches, territory occupancy and density of *S. p. castaneiceps* remained moderately stable throughout the year, much like *D. p. brayanti* (Salgado-Ortiz et al. 2008). This pattern is consistent with other tropical, sedentary birds (Cox 1985; Greenberg and Gradwohl 1986, 1997; Gorrell et al. 2005). I documented only one addition of a territorial pair to a mangrove patch. A higher year round density of males compared to females and pairs may be due to a higher detection rate due to heightened territorial defense.

Territory Switching

Movement of a territorial banded male to another territory was witnessed 8 times (18.6% of re-sighted males). Of these territory movements, all males were seen with a new female. One male was documented to switch his territory to a neighboring territory (abandoning his pair bond), pair with the existing female in that territory, and recruit an additional female which was from another neighboring pair with an absent male. Age is irrelevant in these movements because all individuals were aged as ASY during the re-sighting periods.

Territory switching in year-round territorial tropical birds is both common (e.g. occurred in 37.5 % of known aged Checker-throated Antwrens; Greenberg and Gradwohl 1997) and very responsive to territory vacancies (<1 day) (Levin 1996; Morton et al. 2000). Mangrove Warblers use the most common type of territory such that courtship, mating and nest-building all occurred within the territory boundary, and the young and adults were fed food from within this territory (Welty and Baptista 1988). Territory switching may be due to access to a territory of higher resources or to a mate (Morton et al. 2000; Fedy and Stutchbury 2004). Whether the original territorial males were displaced or died, and resultantly replaced by another individual is unknown.

Removal trials in a sedentary tropical bird (White-bellied Antbird, *Myremeciza longipes*) have shown when adult males were temporarily removed from their territories, some neighboring territorial males switched to the new open territories (Fedy and Stuchbury 2004). Territory switching to increase food availability (Gorrell et al. 2005) and foraging substrate (Morton et al. 2000) has also been recorded in other species of resident territorial birds. This may help to increase adult survivorship and fitness of an individual.

Territory Replacement

I observed high individual replacement throughout the study (53.19% males, 61.90% females). In habitats with stable population density and year-long territorial birds, it is common that vacant territories are filled within a matter of hours (Greenberg and Gradwohl 1997; Morton et al. 2000; Fedy and Stutchbury 2004). In the wintering re-sighting period, I observed many birds throughout the mangrove sites but it is unconfirmed whether these were migrant Yellow Warblers (aestiva group), juvenile Mangrove Warblers, or floaters. It is unknown where or when these individuals moved to the vacant territories, but it is plausible to believe these individuals were floaters. Probable explanations of high occurrence of floaters in these mangrove stands could be due to lack of natal dispersion and emigration, suitable habitat is limited for territory establishment, or possibly as a response to an increase in male population density (Smith et al. 2006), however this would refute the findings that floaters are uncommon in these type of territorial systems (Levin 1996; Morton et al. 2000; Fedy and Stuchbury 2004).

It is possible that the individuals that gained access to the territories were the young from the previous year (as a function of density dependence) (Woolfeden and Fitzpatrick 1984). It is unknown whether the young disperse among mangrove stands, as no juvenile Mangrove Warblers were captured and banded during this study. Salgado Ortiz et al. (2008) found Mangrove Warbler (*D. p. bryanti*) fledglings to remain on natal territories for an average of 27.4 days, however there is no information regarding their movements/dispersal after this time.

Smith et al. (2006) reported 35% territory replacement by first year floaters for a resident island population of Song Sparrows (*Melospiza melodia*). They also reported about 25% of the displaced territory holders became floaters on their previously held territory. Age was found to be important in these territory replacements whereas males 2 and 3 years old (which are both

considered adults) were more likely to take over territories compared to juvenile males and adults 4 years and older.

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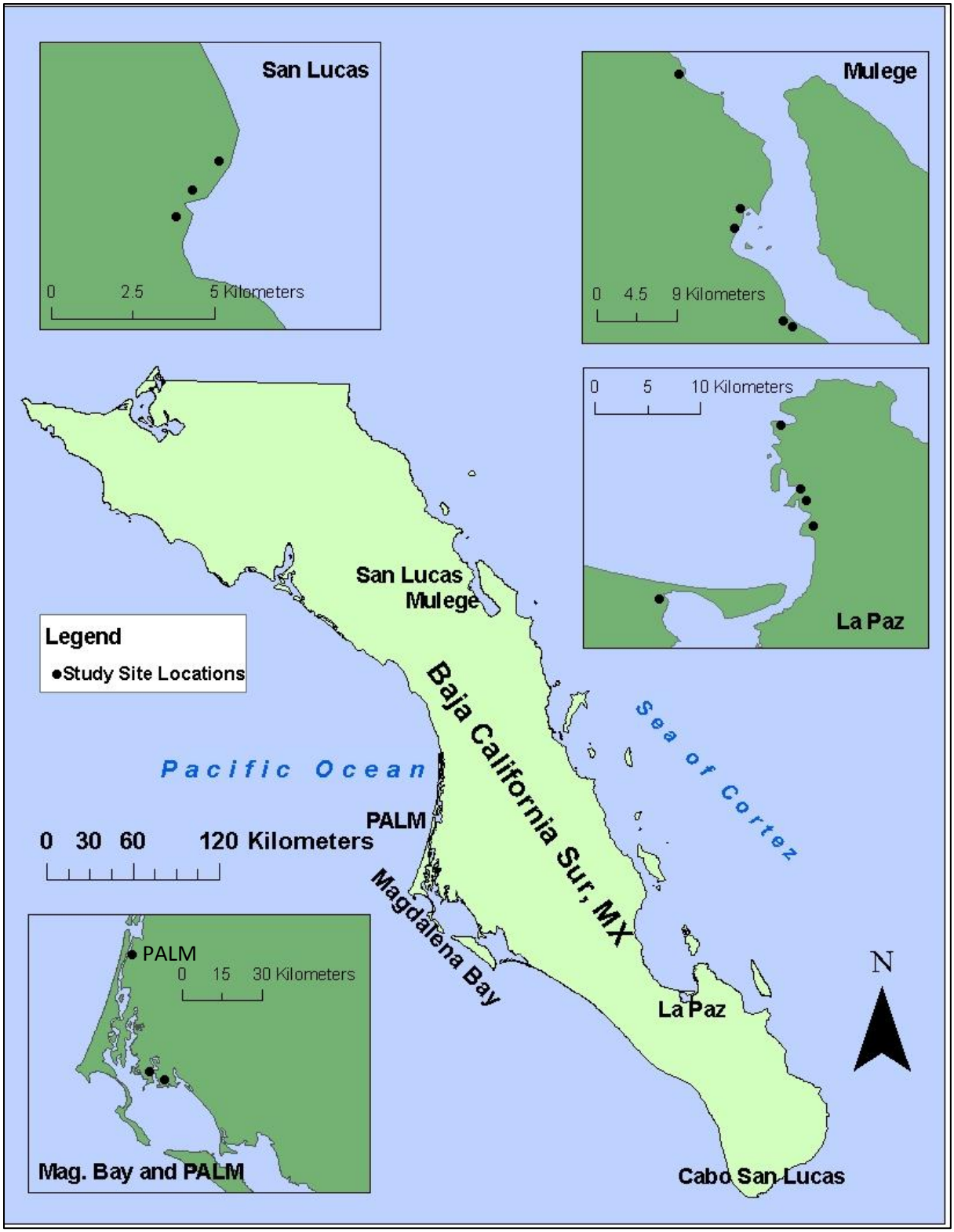

Fig. 1. Five major study areas (San Lucas, Mulegé, Puerto Adolfo López Mateos (PALM), Magdalena Bay, and La Paz) and study site locations in Baja California Sur, Mexico.

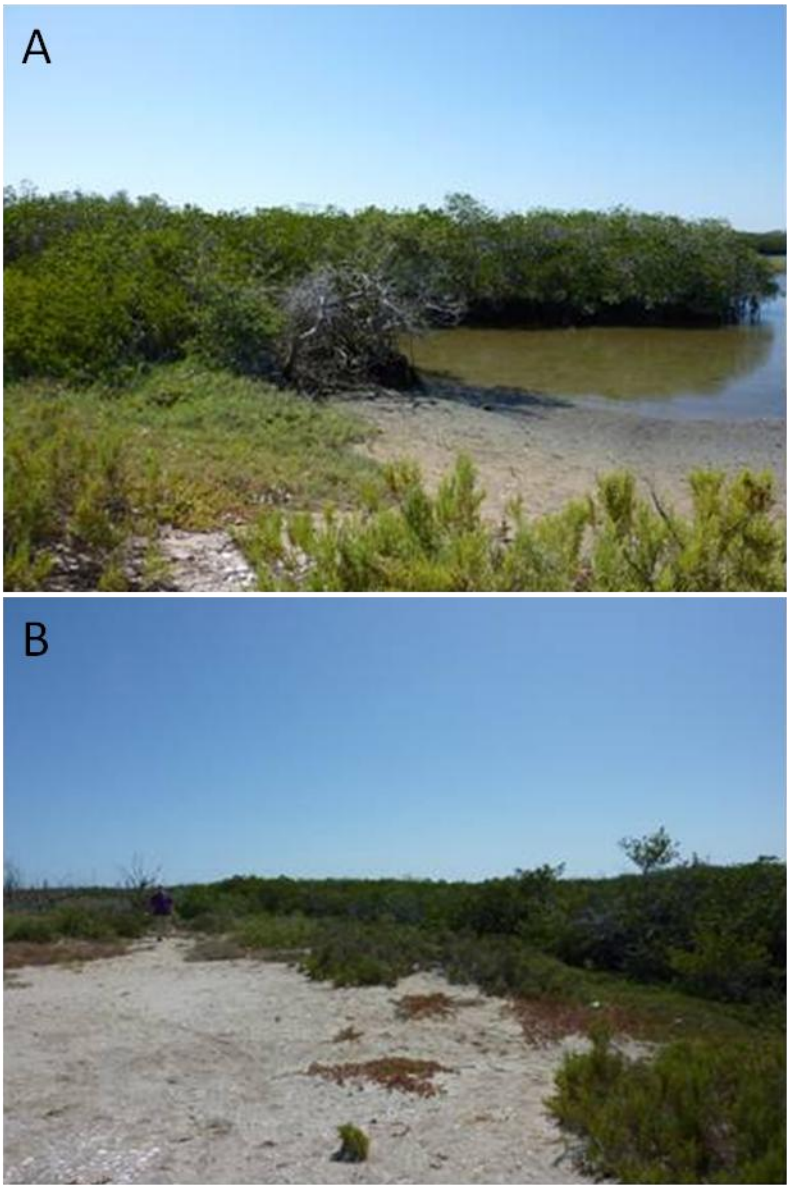

Fig. 2. Magdalena Bay study area, Baja California Sur, Mexico, from lagoon (A) and interior (B).

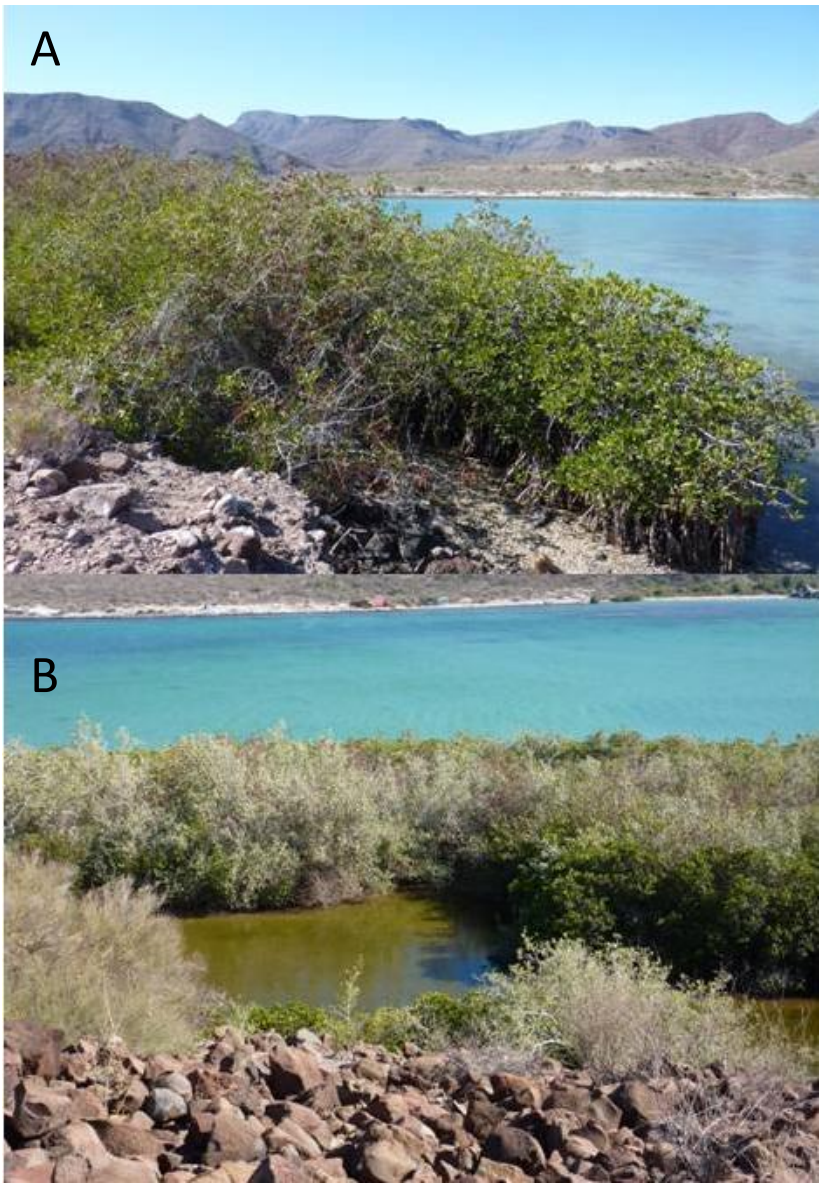

Fig. 3. Mulegé study area, Baja California Sur, Mexico from coast (A) and showing common brackish lagoons within mangrove stands (B).

Fig. 4. San Lucas study area, Baja California Sur, Mexico.

Fig. 5. Puerto Adolfo López Mateos (PALM) study area, Baja California Sur, Mexico from coast at low tide (A) and interior (B).

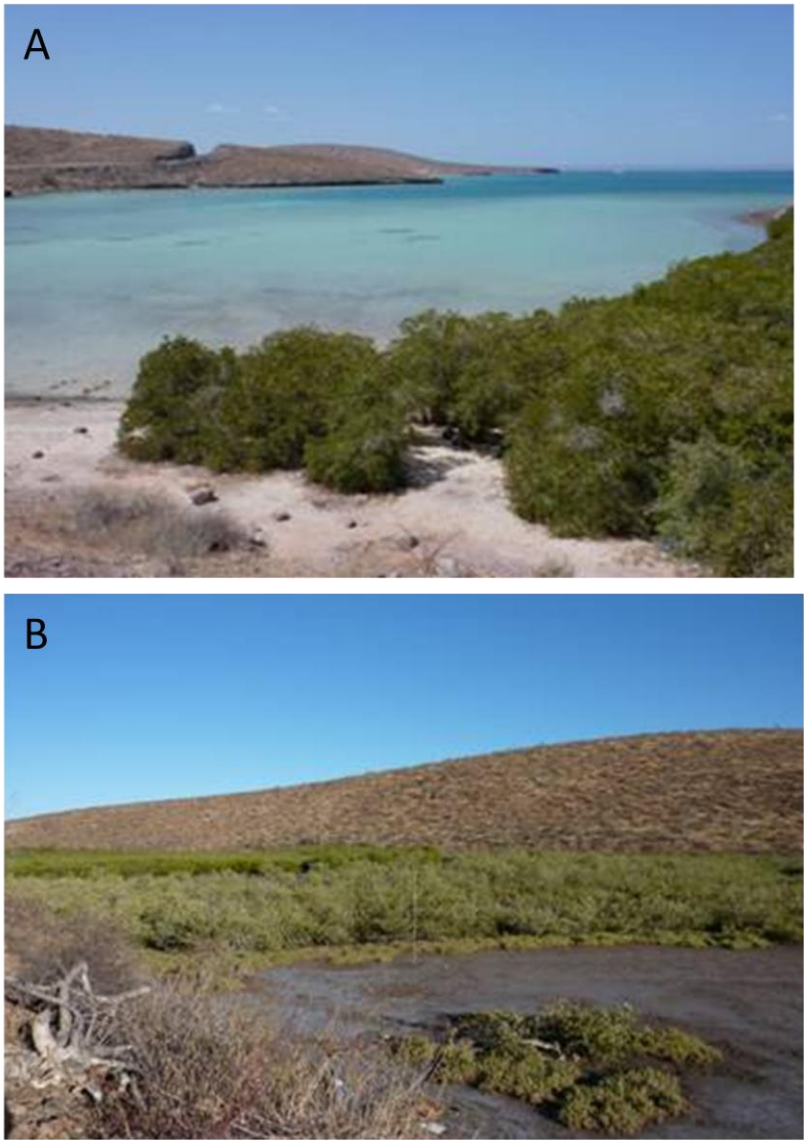

Fig. 6. La Paz study area. Baja California Sur, Mexico from coast (A) and interior (B).

Table 1. Area and perimeter of study areas and study sites in Baja California Sur, Mexico. Straight-line distances between major study areas and minimum/maximum distances between study sites within a study area.

Major Study Area	Study Site Names	Total Area (ha)	Total Perimeter (km)	Max. Distance Between Study Sites (km)	Min. Distance Between Study Sites (km)	Average Distance Between Study Sites (km)
La Paz		40.48	21.04	19.42	0.91	5.72
	LP1	2.37	1.62			
	LP3	3.71	1.62			
	LP4	3.61	2.41			
	LP6	25.05	10.32			
	LP7	5.87	5.07			
Magdalena Bay		67.79	10.39	11.90	11.90	11.90
	MB1	25.87	7.10			
	MB3	41.91	3.29			
PALM		6.46	2.42	--	--	--
Mulegé		8.77	8.53	31.81	1.83	8.01
	MU2	1.41	1.92			
	MU3	0.35	0.73			
	MU4	3.21	2.01			
	MU5	2.92	1.94			
	MU6	0.88	1.93			
San Lucas		4.04	3.30	1.94	0.95	0.95
	SL1	0.17	0.17			
	SL2	1.74	1.26			
	SL3	2.12	1.87			

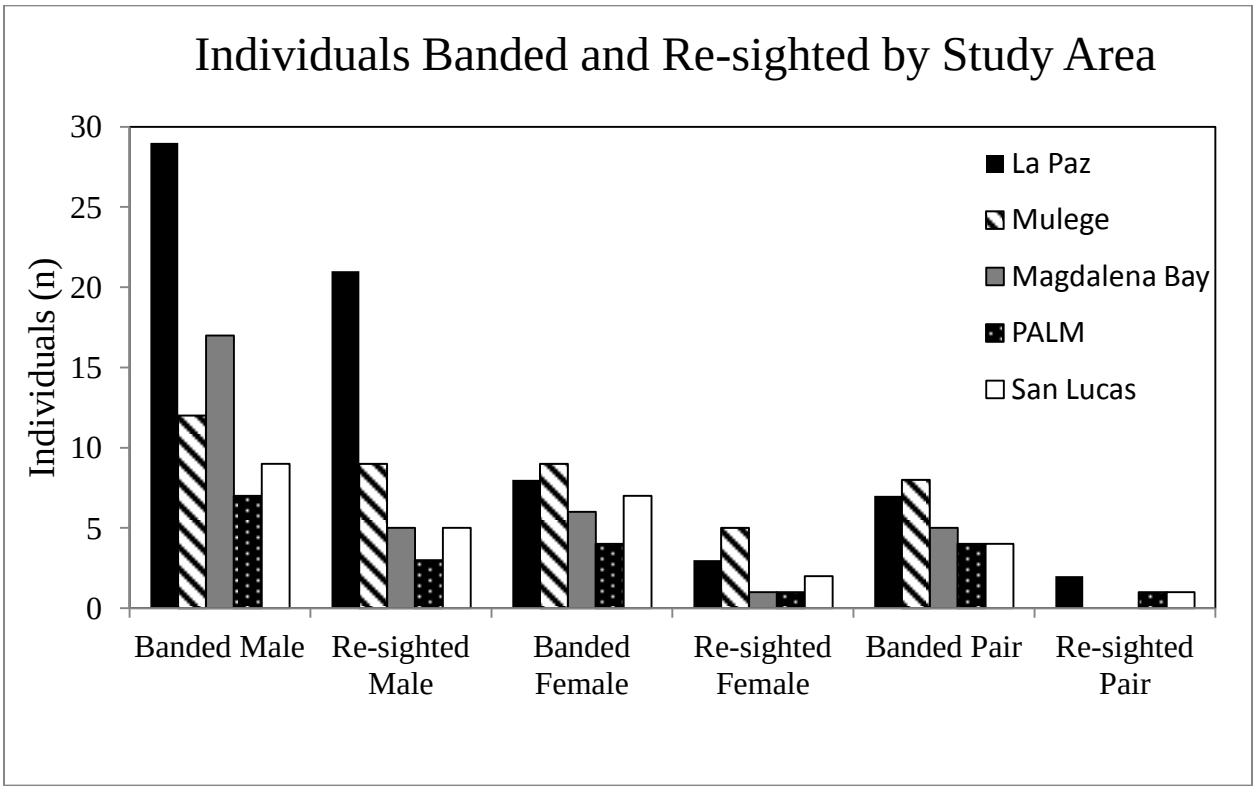

Fig. 7. Number of individuals and pairs banded (2010) and re-sighted (2010, 2011) in the major study areas.

Table 2. Percent re-sights of male and female Mangrove Warblers during different periods by study area and study site in Baja California Sur, Mexico.

Study Area	Study Site	Wintering (Nov. 2010)				Spring (Apr. 2011)				Overall (Nov. 2010 and Apr. 2011)	
		% Re-sighted by Effort		% Re-sighted of Total Banded Population		% Re-sighted by Effort		% Re-sighted of Total Banded Population		% Re-sighted of Total Banded Population	
		Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
La Paz		58.30	33.3	48.3	25.0	48.3	12.5	48.3	12.5	66.7	37.5
	LP1	0	0	0	0	0	0	0	0	0	0
	LP3	100	—	100	—	50	—	50	—	100	—
	LP4	100	50	100	50	100	0	100	0	100	50
	LP6	63.6	100	58.3	33.3	50	0	50	0	83.3	33.3
	LP7	16.7	0	10	0	30	50	30	50	40	50
Mag. Bay		11.8	0	11.1	0	27.8	28.6	27.8	28.6	27.8	28.6
	MB1	15.4	0	15.4	0	23.1	0	23.1	0	23.1	0
	MB3	0	0	0	0	40	66.7	40	66.7	40	66.7
PALM		—	—	—	—	42.9	25	42.9	25	42.9	25
Mulegé		40	12.5	33.3	11.1	50	55.6	50	55.6	75	55.6
	MU2	60	0	60	0	40	100	40	100	80	100
	MU3	0	50	0	50	100	50	100	50	100	50
	MU4	100	0	33.3	0	33.3	50	33.3	50	66.7	50
	MU5	0	0	0	0	50	0	50	0	50	0
	MU6	0	0	0	0	100	0	100	0	100	0
San Lucas		11.1	16.7	11.1	14.3	33.3	28.6	33.3	28.6	44.4	28.6
	SL1	0	0	0	0	0	0	0	0	0	0
	SL2	33.3	50	33.3	50	33.3	100	33.3	100	66.7	100
	SL3	0	0	0	0	40	0	40	0	40	0
Total		37.3	20	29.7	14.7	43.2	32.4	43.2	32.4	58.1	38.2

Table 3. Population density (# of individuals/ha) of *S. p. castaneiceps* across study areas and study sites, Baja California Sur, Mexico.

Study Area	Study Site	Breeding 2010			Wintering 2010			Breeding 2011		
		Male	Female	Pairs	Male	Female	Pairs	Male	Female	Pairs
La Paz		0.72	0.22	0.22	0.72	0.37	0.35	0.47	0.32	0.42
	LP1	0.42	0.42	0.42	1.27	0.84	0.84	0.42	0	0
	LP3	0.54	0	0	0.54	0.27	0.27	0.27	0.54	0.27
	LP4	1.11	0.55	0.55	2.77	1.39	1.39	1.94	0.83	0.83
	LP6	0.48	0.16	0.16	0.36	0.24	0.20	0.40	0.32	0.32
	LP7	1.70	0.34	0.34	0.85	0.17	0.17	1.02	0.85	0.85
Magdalena Bay		0.27	0.10	0.10	0.15	0.10	0.10	0.13	0.13	0.13
	MB1	0.50	0.15	0.15	0.35	0.23	0.23	0.23	0.19	0.19
	MB3	0.12	0.07	0.07	0.02	0.02	0.02	0.07	0.10	0.10
PALM		1.08	0.62	0.62	na	na	na	0.77	0.77	0.77
Mulegé		1.37	1.03	0.91	0.91	0.23	0.23	1.14	1.14	1.14
	MU2	3.55	2.13	2.13	2.13	0	0	2.13	2.84	2.84
	MU3	2.86	5.71	2.86	2.86	2.86	2.86	2.86	2.86	2.86
	MU4	0.93	0.62	0.62	0.62	0	0	0.93	0.93	0.93
	MU5	0.68	0.34	0.34	0.34	0	0	0.68	0.34	0.34
	MU6	1.14	1.14	1.14	1.14	1.14	1.14	1.14	1.14	1.14
San Lucas		2.23	1.73	1.73	1.49	0.99	0.99	0.99	0.99	0.99
	SL1	5.88	5.88	5.88	5.88	0	0	0	0	0
	SL2	1.72	1.15	1.15	1.72	1.72	1.72	1.15	1.15	1.15
	SL3	2.36	1.89	1.89	0.94	0.47	0.47	0.94	0.94	0.94

Table 4. Repeated measures ANOVA table (using Autoregressive 1 covariance structure) comparing population densities among sex (Male, Female, Pair), season (Breeding 2010, Wintering 2010, Breeding 2011), and the interaction of sex and season.

Type 3 Test of Fixed Effects				
Effect	Num dF	Den dF	F Value	Pr>F
Sex	2	132	4.27	0.02
Season	2	132	2.72	0.07
Sex*Season	4	132	0.85	0.50

Fig. 8. Boxplots of *S. p. castaneiceps* density (birds/ha) by sex (F=female, M=male, P=pair) across the combined seasons of Breeding 2010, Wintering 2010 and Breeding 2011.

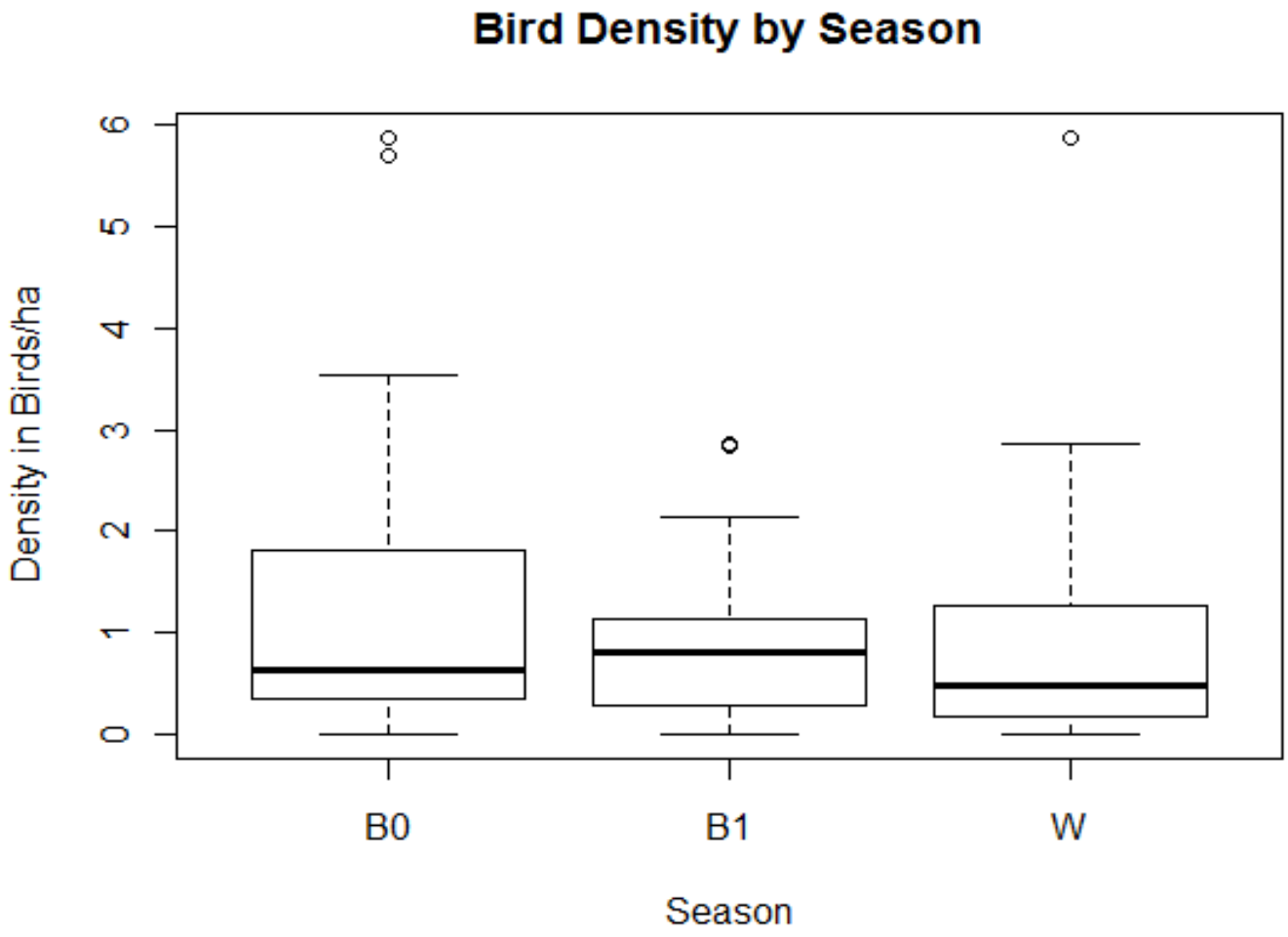

Fig. 9. Boxplots of *S. p. castaneiceps* density (birds/ha) by season (B0= Breeding 2010, B1= Breeding 2011, and W=Wintering 2010) across the combined sexes of males, females and pairs.

Table 5. Territory switching in banded territorial adults observed during both re-sighting periods. All distances are straight line between an individual's observed locations. Study site refers to individual mangrove within major study area (LP, La Paz; Puerto Adolfo López Mateos, PALM; MU, Mulegé; SL, San Lucas).

Band Combo	Sex	Study Site	Distance Moved (km)
BM:BBB	M	LP6	1.55
BM:GGG	M	LP6	0.55
BM:GBY	M	LP6	1.2
RM:GRG	M	PALM	0.43
GM:GYB	M	MU2	0.91
GM:GYR	M	MU2	0.31
GM:GBR	F	MU2	0.21
GM:BGR	M	MU4	0.03
GM:BRR	M	SL3	0.11

Table 6. Territory replacements of territorial, banded adults occurring within mangrove patches throughout the re-sighting periods. Territory vacancies refers to territories in which a previously territorial individual was not re-sighted.

	Male	Female	Total
Territory Vacancies	47	21	68
Filled by Banded	7	1	8
Filled by Unbanded	25	13	38